FIVE Paleozoic Terrestrial Ecosystems

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IN COLLABORATION WITH
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1 INTRODUCTION

The Paleozoic records the origin, assembly, and modernization of terrestrial ecosystems. Significant ecological and evolutionary events included the colonization of land by nonvascular plants, the appearance and diversification of vascular plants, the radiation of terrestrial arthropods, the origin of air-breathing vertebrates, the rise of amniotes, and the development of tetrapod herbivory. These events, occurring within ecological frameworks fundamentally different from any that came later, appear almost directional when viewed in retrospect. Paleozoic ecosystems progressed, although not continuously or necessarily gradually, toward a modern system of interactions among primary producers, arthropod and tetrapod detritivores and herbivores, and predatory animals during a period of approximately 200 million years. By the Late Permian, ecosystem structure and dynamics were not substantially different from those of the present day, even though all the species were different.

The major events that occurred during the Paleozoic dictated the future course of ecological and evolutionary history in the terrestrial biosphere. Consequently the Paleozoic can be visualized as a time of "canalization" or entrenchment of the major kinds of interactions among organisms and environments at the ecosystem level. As ecosystems became more complex, the existing spectra of interactions and ecological opportunities confined the course of subsequent events, both ecological and evolutionary. It also was a time of establishment of the basic patterns of physiological ecology of terrestrial organisms, including water and nutrient acquisition and transport in plants, means of acquiring and processing food in animals, and other biological attributes still found in the present-day biota. Yet the apparent directionality of these patterns is belied by detailed examination. The Paleozoic illustrates, perhaps better than any other time, how the ecosystems and the species that comprised them interacted, placing increasingly narrow limits on the course of subsequent evolutionary events.

Our objective is to integrate plant and animal fossil records. Differences in the nature of these records quickly become obvious, and there are few fossil deposits where both abundant plant and animal remains co-occur. Within much of the late Paleozoic, plant localities are abundant, and both macrofossils and microfossils can be sampled. Plants frequently are transported only limited distances (Gastaldo 1988; chap. 2), thereby permitting certain parts of the original landscape to be reconstructed. Paleozoic animal occurrences, however, are usually sufficiently rare and widely spaced stratigraphically to provide only glimpses of animal assemblages, often rendering community reconstruction problematic.

Inferences of function, on the other hand, can be drawn far more readily for individual animals than for many plants. The preservation of even fragmentary animal hard parts may offer information on feeding mechanisms, food preference, and motility. In contrast, fragmentary plant material can be difficult to place in a whole-plant context, which is necessary for inference about life history and ecological strategy. Even whole plants may be uninformative in the lack of quantitative data on population dynamics and habitat preferences. This is particularly true of Paleozoic plants for which closely related modern descendants, or even potential modern ecological analogues, are lacking.

Because co-occurrences are limited, and because the interactions between plants and animals and their environments (herbivory, detritivory, structural and chemical defenses, habitat and space requirements, etc.) are difficult or impossible to observe in the fossil record, integration relies on our ability to build scenarios consistent with the data. We do not hope to reconstruct what happened point by point but rather focus on broad time intervals and describe the components and their possible interactions. Through comparison of inferred structural and dynamic features of ecosystems from different time intervals, it is possible to evaluate these systems for properties that are independent of taxonomic composition.

Prior to the Late Silurian, all inferences for terrestrial ecosystems are made from indirect evidence. This evidence comes primarily from analysis of paleosols and from studies of the microbial biota of time-equivalent marine facies. From the Late Silurian onward, however, there is unequivocal megafossil evidence of terrestrially adapted plants and animals, as well as rhizome or rootlike traces and invertebrate burrows in the upper horizons of paleosols. Such paleosols also provide evidence of chemical zonation and organic enrichment attributable to a terrestrial community. Prior to the Late Silurian, from rocks of Late Ordovician to mid-Silurian age, there are abundant remains of plants or plantlike organisms that share many of the organizational properties of "true" land plants (here meaning embryophytes). These constitute compelling evidence for a terrestrial biota rich in primary producers, but of uncertain taxonomic affinities.

2 THE ORDOVICIAN

Evidence for an Ordovician terrestrial biota is conclusive, although the exact nature of its constituents remains conjectural. Paleosols from the Dunn Point Formation of Nova Scotia show reduction mottles and surficial erosion patterns that suggest soil formation and stabilization by clumps of nonvascular plants; rooting structures, however, are not preserved (Retallack 1981, 1986a).

Studies of paleosols from the Juniata Formation of Pennsylvania led Retallack (1985a, 1985b) and Feakes and Retallack (1988) to describe fossil soils from two contrasting environments. One series comprised immature soils formed along streamsides, whereas the other formed on low terraces and was more mature. Both show reduction mottles indicative of bacterial modification of organic matter, chemical profiles suggestive of plant colonization, and burrows of presumed arthropod origin (Retallack and Feakes 1987). Overall the Ordovician landscape of tropical paleolatitudes was relatively barren, with a low-diversity and sparsely clumped low-growing vegetation and a few invertebrates (Feakes and Retallack 1988).

Further evidence of the vegetation of this time comes from analyses of the microfossil record from near-shore marine sediments (Gray 1985). These include obligate spore tetrads, reminiscent of some modern liverworts, as well as sheets of tissue from enigmatic nematophytalean plants (nonvascular plants of uncertain affinity). These data suggest that the first major adaptive radiation by plants onto land occurred in Middle to Late Ordovician and involved plants at or near the nonvascular grade of vegetative organization. These might have included bryophytic plants, lichens, and fungi, in addition to the microbial mats that probably existed on land since the Late Precambrian. The Middle to Late Ordovician may have been an interval of rapid colonization by founding populations with limited genetic diversity (indicated by the monotony of the obligate spore tetrads), with life histories that included ecophysiological tolerance to desiccation, and with short vegetative life cycles (Gray 1985). Judged from their ubiquitous occurrence in deposits of this age, such forms occurred worldwide.

3 THE SILURIAN

The evidence for an Early Silurian terrestrial biota consists mainly of the same varieties of microfossils reported by Gray (1985) in the Ordovician. Beginning in mid–late Early Silurian, however, obligate spore tetrads of uniform morphology were replaced by trilete spores (single spores with a mark on one face, formed by being pressed together in a tetrahedral tetrad following meiosis) (Pratt et al. 1978). These diversified rapidly in ornamentation and laesural morphology (shape of the trilete mark), perhaps indicating a second major radiation as plants approached and attained the vascular plant grade of vegetative organization (Gray 1985). The diversity of spore types that appeared during this second radiation suggests establishment of large populations of plants and greater intertaxon variation (Gray 1985).

The microfossil record agrees well with the appearance of megafossils (Edwards 1980; Edwards and Fanning 1985) in the middle Silurian (Wenlockian) (see fig. 5.1 for stratigraphic chart) and the gradual diversification into the latest Silurian (Pridolian) of a flora consisting largely of *Cooksonia*- or *Salopella*-like rhyniophytes (very simple, possibly nonvascular, sticklike,

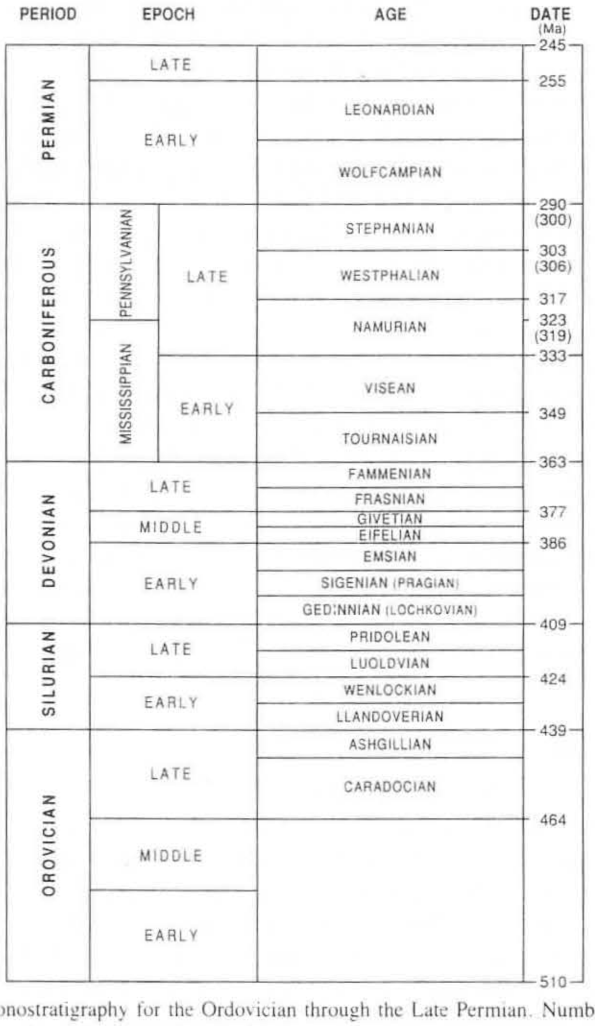


Fig. 5.1. Chronostratigraphy for the Ordovician through the Late Permian. Numbers in parentheses are alternative dates for age boundaries.

rootless and leafless plants with terminal sporangia). Whereas the early rhyniophyte floras are typical of Euramerican deposits, an approximately coeval flora has been found in Australia that includes a complex vascular plant, *Baragwanathia* (Timms and Chambers 1984). Because *Baragwanathia* is a lycopsid with true roots and leaves, it is more advanced morphologically than any plant of comparable age from Euramerica, which has led to doubts regarding its age (Bateman 1991; Hueber 1992), determined from associated graptolites (Garratt and Rickards 1984). Should future studies support the Silurian determination, *Baragwanathia* will place the evolution of Gondwanan vegetation considerably ahead of that of Euramerica.

Most Silurian floras occur in marine facies. When found in terrestrial beds, the fossils occur most often in fluvial sandstones (Edwards 1980; Edwards and Fanning 1985). The few plant axes found in laterally equivalent floodplain deposits also are allochthonous, and there is no direct evidence for plant communities (Edwards and Fanning 1985) except for those inferred from analysis of Silurian paleosols.

Retallack (1985a, 1986) described a Late Silurian (Ludlovian) paleosol from Pennsylvania that has structures similar to rhizome traces of an early vascular plant, such as a rhyniophyte. This paleosol is reported to be much better developed than the Ordovician examples noted above (Retallack 1986). Although the evidence is sparse, Retallack concluded that a variety of poorly known, nonvascular plants preceded primitive vascular plants on land, and that large soil animals of uncertain affinities were present. The discovery of Late Silurian terrestrial predatory forms, trigonotarbid arachnids and centipedes (Jeram et al. 1990), lends weight to this speculation, in that predatory invertebrates indicate the existence of simple food webs that would have included nonpredatory forms. Based on present knowledge of Early Devonian biotas, the Silurian food webs probably were based on as yet unknown detritivores or grazers that fed on microorganisms.

Ecological reconstruction of Silurian plant communities can be derived from the architecture of the fragments and their sedimentological context; further environmental inferences can be based on paleosol data. Axes are small and fork at wide angles, and all terminal parts end in sporangia. Floodplain deposits show fewer, but larger axes, whereas channel sandstones show abundant, fragmentary small axes, often almost completely covering ripple surfaces, along with rounded pieces of silicified *Prototaxites*. Many paleosols are reported to contain calcareous nodules that may represent pedogenic carbonates indicative of low sedimentation rates and possibly long-term subaerial exposure (see chap. 2).

Edwards (1980) concludes that *Cooksonia* and similar plants probably produced little cover of any height because every aerial axis tip was determinate and ended in a sporangium. Edwards and Fanning (1985) speculate that in such an ecosystem, in which active river systems were flanked by broad, well-drained floodplains, plants probably grew adjacent to the channels and also on bar tops. They further suggest the possibility that the simplicity of these early plants may not be primitive but may reflect reduction associated with adaptation to either swamp or arid, edaphically stressed environments. Mummified axes and sporangia, for example, show extensive sclerenchyma (thick-walled cells) in the outer layers of axes, an anatomical modification often found in plants from either kind of habitat. These plants, however, may have been nonvascular; in this case the cortical cells would have provided the principal support, confounding a uniformitarian comparison and inference.

Using paleogeographic reconstructions (see figure 5.2) and sedimentological analyses, Edwards and Fanning (1985) suggest that the plants of relatively unstable floodplain environments in warm and seasonally dry climates may have been opportunists with rapid sexual maturation of gametophytes in the wet season; this resulted in early establishment of more drought-tolerant sporophytes. Plants like *Cooksonia* and *Salopella* expended minimal energy in vegetative growth and quickly reached simultaneous spore production from determinate aerial branches. A single plant may have covered a large area by rhizomatous growth resulting in a patchy vegetation dominated locally by just one species.

Sherwood-Pike and Gray (1985) describe probable ascomycete hyphae from Late Silurian (Ludlow) strata. They suggest that these were terrestrial fungi at least contemporaneous with the earliest land plants. Some hyphae occurred inside small rounded pellets of apparent invertebrate fecal material; if this is correct, it suggests a fauna that included mycophagous (fungus-eating) microarthropods. Rolfe (1985b) accepts this suggestion and identifies millipeds from Late Silurian (Ludlow-Pridoli), now complemented by the discovery of predatory animals (Jeram et al. 1990). The importance of these observations is that they confirm at least a minimal terrestrial food web consisting of primary producers, decomposers, secondary consumers, and predators.

4 THE EARLY TO MIDDLE DEVONIAN

Lower to lower Middle Devonian rocks provide the first adequate glimpse of terrestrial ecosystems from numerous sites around the world. Most of the continental land surface was in the southern hemisphere (Boucot and Gray 1983; Scotese in Gensel and Andrews 1984; Livermore et al. 1985; Scotese et al. 1985) (Figure 5.2 illustrates inferred continental positions in the Late Silurian). The known fossiliferous deposits are mostly from wetland habitats in tropical and subtropical regions, although some are known from higher latitudes (Gensel and Andrews 1984; Raymond et al. 1985a).

Floras appear to have been relatively cosmopolitan, with some distinctions apparently a consequence of physical barriers and latitudinal, possibly climatic, factors (Timms and Chambers 1984; Raymond et al. 1985a). Edwards and Fanning (1985), however, conclude that such generalizations on the early biogeography of vascular plants are premature because assemblages from elsewhere in the world generally are poorly preserved and are not independently dated, making detection of provincialism in the Late Silurian and Early Devonian difficult. They disagree specifically with Ziegler et al. (1981), who identify three floral units. Raymond et al. (1985a) find a pattern similar to that of Ziegler et al. (1981) for the late Early Devonian (middle Siegenian-Emsian), including (1) a large equatorial and low latitude unit that includes floral assemblages from China, Kazakhstan, Siberia, Laurussia, and northern Gondwana; (2) a small southern low-latitude unit that includes assemblages from Australia; and (3) a small middle-to-high latitude unit that includes floral assemblages from South Africa and Australia. For early Early Devonian (Gedinnian–Early Siegenian), in contrast, Raymond et al. (1985a) find just two poorly differentiated units: (1) an Australian unit characterized by *Yarravia* and *Baragwanathia;* and (2) a widespread "northern hemisphere" unit characterized by *Zosterophyllum, Taeniocrada, Cooksonia,* and *Drepanophycus.* Note, however, that floras from China, which are only now being studied in full, contain many plants not seen elsewhere in the Northern Hemisphere.

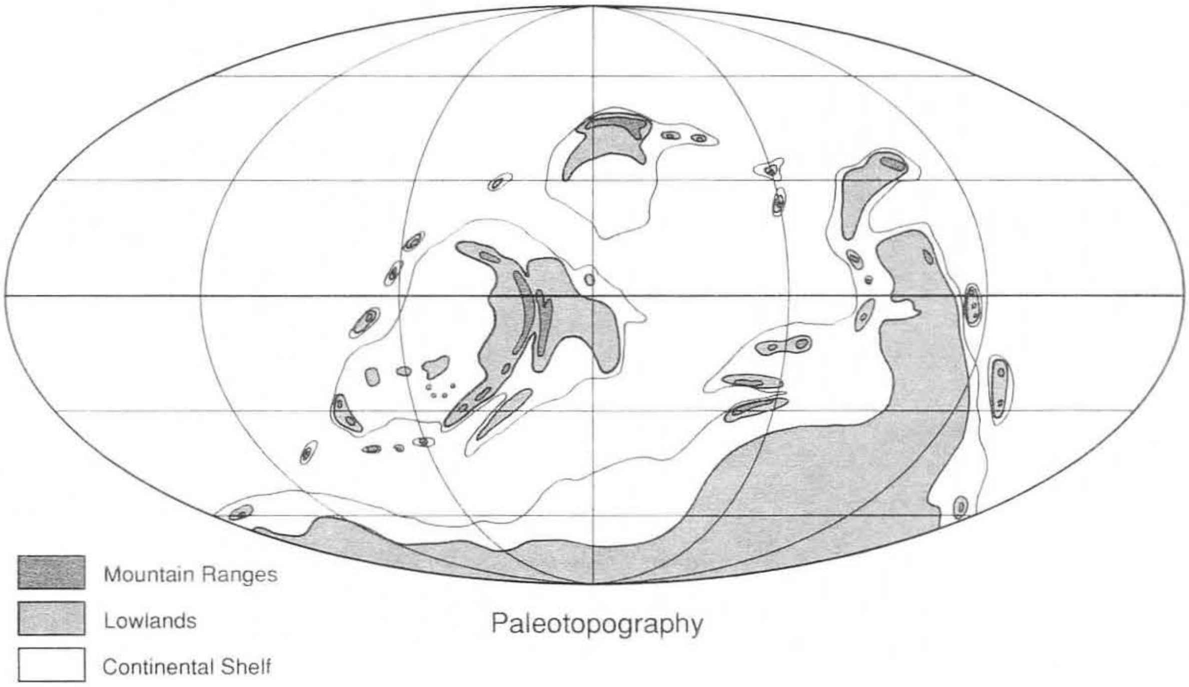
Animals are known from only a few localities, and faunas may have been morphologically simple and of rather low diversity. At present no biogeographic patterns can be detected.

4.1 Plants

Diversification of vascular plants accelerated in the Early Devonian. During Gedinnian time (fig. 5.1) a new clade, the zosterophylls, had appeared; by Siegenian (Pragian) time, two more, the lycopsids and trimerophytes, were present. The new morphologies and morphological combinations represented by these clades provided opportunities for still-further diversification and added new architectures to terrestrial landscapes, making community structure and dynamics more complex. Examples of these architectural innovations include pseudomonopodial growth (a "main trunk") secondary vascular tissues that transported nutrients and added support, thus permitting taller plants, and root systems that supplemented and amplified the anchorage and absorptive capacities needed by larger plants. Reconstructions of many of these plants are provided by Gensel and Andrews (1984).

The Late Silurian and Early Devonian rhyniophytes and zosterophylls were small plants that formed local, monospecific patches as a result of clonal growth. Most spread vegetatively by the growth of prostrate axes from which aerial axes arose (Niklas and O'Rourke 1982; Tiffney and Niklas 1985). Where known, these all had only tufts of rhizoids on the bottoms of their horizontal axes, which provided anchorage and permitted absorption (Kidston and Lang 1917, 1920a, 1921a; Gensel et al. 1975; Hueber and Banks 1979;

LATE SILURIAN (425 Ma)



Paleotopography

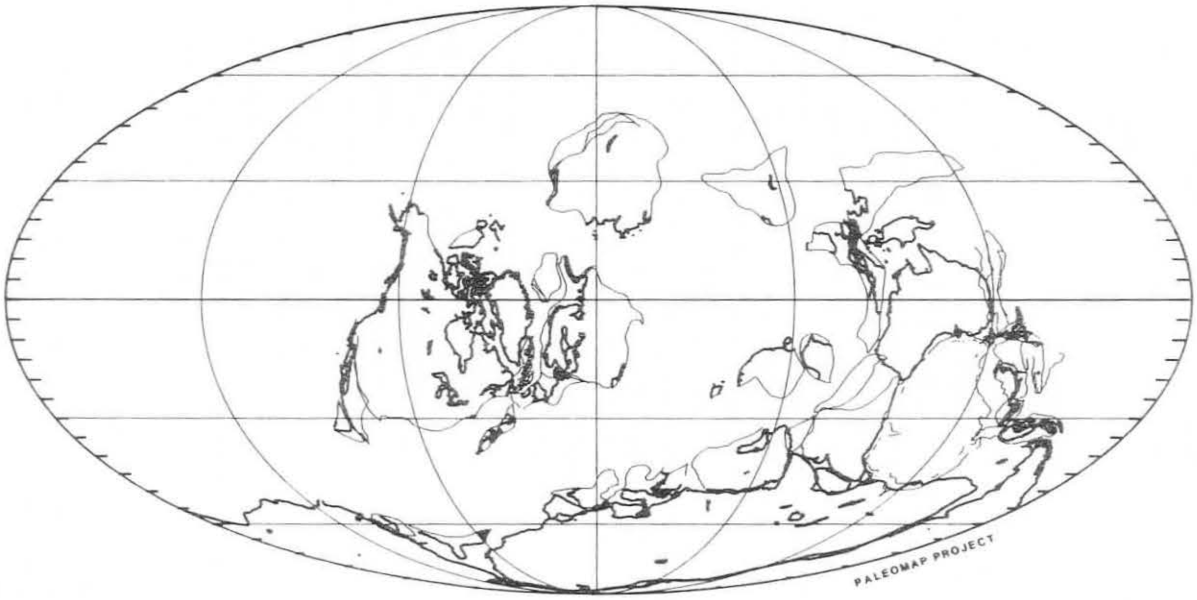


Fig. 5.2. Generalized continental positions and orography in the Late Silurian. (Courtesy of C. R. Scotese and the PaleoMap Project, University of Texas, Arlington.)

Rayner 1983; Banks 1985). Rhizoids had only limited ability to penetrate the substrate to acquire water and nutrients, a problem possibly ameliorated by mycorrhizal associations (Pirozynski and Malloch 1975; Malloch et al. 1980). Thus, they were able to utilize only surface water and were probably limited to habitats characterized by nearly continuous moisture. Water conductance was limited by reliance on rhizoids as well as by the presence of few stomata on the aerial parts.

The middle Early Devonian (Siegenian) trimerophytes had complex branching patterns. The aerial shoot was composed of tall main axes that bore highly dichotomized lateral branches. Lycopsids had leafy aerial axes borne on rhizomes that also produced sparse, small forked roots that penetrated soils (Kidston and Lang 1920b, 1921a; Tanner 1983; Rayner 1984). According to Remy et al. (1980b), root penetration of floodplain sediments did not occur until the Siegenian, after which root traces and their effects on paleosols are common. For the first time, subsurface water and nutrients could be utilized, so that slightly drier habitats might be colonized. Trimerophytes are not yet known to have had root systems, although their xylem was thicker and evidences somewhat extended production of vascular tissues. Their large size (some *Pertica* species are 2 m tall) suggests substantial transpirational demands (compared to earlier plants), which may have required roots. Aerial axes in most of these plants varied from leafless to spiny to being densely covered with short leaves; in all cases there was relatively little surface area for photosynthesis and small biomass, suggesting relatively low requirements for water, CO_2, and mineral nutrients.

All Early Devonian vascular plants were homosporous. This entails a life history in which the diploid sporophyte alternates with a free-living, haploid, sexual phase, the gametophyte. The Devonian gametophytes that have been reported (Remy 1982; Remy and Remy 1980a; Remy et al. 1980a, b; Remy et al. 1991; Schweitzer 1980, 1981) suggest that water-mediated fertilization was the rule, as in modern, free-sporing plants. Some of these gametophytes are quite large, and those of the Rhyniophytes in particular suggest an isomorphic alternation of generations (Remy and Hass 1991 a, b, c; Kenrick and Crane 1991). In general, spore production and subsequent gametophytically mediated sexual reproduction may have been most important in dispersal and location of new sites, whereas clonal growth was the major means by which established plants expanded within local habitats. Sporangium-bearing axes are relatively uncommon in many species, and productivity in these plants probably was very low (Beerbower 1985).

Early terrestrial plant communities were quite simple in structure and dynamics, regardless of taxonomic composition and geographic variation. Landscape diversity was low; at most 10 to 15 genera (many represented by a single species) comprised a flora drawn generally from a range of habitats (Gensel and Andrews 1984; Knoll et al. 1984; Niklas et al. 1985). Exposure-scale or single-bed collections generally have still lower diversity, 1 to 5 species (Bateman, in press), suggesting limited interhabitat interactions. Both vascular and nonvascular plants made up the vegetation. The time of appearance of true tracheophytes is equivocal. Depending in part on how tracheary cells are defined (Kenrick, Edwards, and Dales 1991; Kenrick, Remy, and Crane 1991; Kenrick and Crane 1991), many plants originally considered to have been vascular plants in fact may be nonvascular but share other derived features with early tracheophytes. Included are well-known plants such as *Cooksonia* (Edwards and Edwards 1986) and *Aglaophyton (Rhynia) major* (Edwards 1986). Kenrick and Crane (1991) also argue for a group of early tracheophytes with water-conducting cells distinct histologically from other tracheophytes. This diversity of vascular and nonvascular plants—of which many were distinct morphologically from tracheophytes but contributed significantly to early land vegetation (Gray 1985; Taylor 1982)—gives floras from this time an unusual degree of heterogeneity at the highest taxonomic levels.

Plants that form the record of this time occupied predominantly wetland areas and the margins of watercourses where substrates were wet much of the time (Diane Edwards 1980; Schweitzer 1983; Beerbower 1985). Canopy heights were low (less than 2 m) and evidence of stratification—more than one layer of vegetation—is equivocal.

Early Devonian plant communities usually consisted of an array of patches, each patch dominated by a single species (Andrews et al. 1977; Diane Edwards 1980; Edwards and Fanning 1985). An example is the Trout Valley flora of Maine (Andrews et al. 1977), which Gensel and Andrews (1984) considered typical of many Early Devonian assemblages. Vegetation consisted of low-diversity patches; patch size varied but usually was composed of one to three or four species. It is probable that patches were occupied by large clones, within which sexual reproduction was relatively rare (Edwards and Fanning 1985). Knoll et al. (1979) refer to this pattern of space occupation as "turfing in." Because these early land plants had limited capacity to obtain nutrients from the substrate and limited potential for vertical growth (Niklas 1982), a space-occupation strategy permitted them to control access to water and nutrients, as well as to compensate for limited photosynthetic area. At some localities, certain species appear to occur most often in specific lithologies, suggesting habitat or microhabitat specificity among groups of species. This raises the issue of how to delimit communities in the Early Devonian. Interactions between clones at the margins of patches and competition during the location and initial exploitation of new sites may have been the major types of plant-plant dynamics; this suggests landscape-level processes similar to those found today in disturbed settings.

The expansion and diversification of plants in the Early Devonian also had an effect on the dynamics of floodplains and on edaphic properties of ecosystems. Secondary succession, manifested as vegetational recovery following ecosystem disturbance, became dominant over the primary successional colonization of previously unoccupied surfaces. Bank-dwelling plants may have acted to stabilize stream courses, thereby lessening the effects or frequency of flooding. In general, soil formation was less often and less critically interrupted by clastic sedimentation (Retallack 1981), although flood disturbance remained a major modifier of ecosystem patterns (Andrews et al. 1977). With the development of large stands of plants with tree habit in the Middle and Late Devonian, even greater portions of the landscape would have been stabilized.

Our considerable morphological knowledge of Devonian plants enables us to infer how their architecture or reproduction affected their ecology. Many occurrences of Early Devonian zosterophylls, lycopsids, or trimerophytes are preserved in near-channel, overbank deposits in which parallel alignment of numerous axes of a single species suggest that "the plants grew in dense monotypic water-side stands that were flattened by sudden floods" (Edwards and Fanning 1985; other examples in Andrews et al. 1977; Diane Edwards 1980; Gensel 1982; Gensel and Andrews 1987). The rhizomatous habit from which aerial axes arose and propagated is now firmly established in all the major clades: rhyniophytes (Kidston and Lang 1917, 1920a, 1921a), trimerophytes (Doran 1980), zosterophylls (Lang 1927; Lele and Walton 1961; Gensel et al. 1975; Hueber and Banks 1979; Rayner 1983), and lycopsids (Kidston and Lang 1920b, 1921a; Gensel et al. 1969; Rayner 1984).

In situ preservation of monocultures of *Rhynia, Horneophyton, Aglaophyton,* and *Lyonophyton* occurs in the permineralized peat of the Rhynie Chert (Kidston and Lang 1917, 1920a, 1921b; Remy 1982; Remy and Remy 1980a, 1980b; Bateman in press). *Sciadophyton,* a probable branched gametophyte, is preserved in situ in floodplain sediments (Remy et al. 1980a, 1980b).

A consistent image emerges from studies of Devonian plants and their habitats, one of evolving terrestrial ecosystems, driven by plant evolution itself. Summaries are found in Diane Edwards (1980), Scott (1980), Edwards and Fanning (1985), and Collinson and Scott (1987a).

4.2 Animals

Virtually all terrestrial animal fossils from the Early Devonian are arthropods. A quadrupedal trackway has been reported from Australia (Warren et al. 1986), but its affinities are unclear, and actual remains of terrestrial vertebrates are unknown in rocks of this age. Arthropod assemblages are reconstructed from a few well-studied localities and several isolated occurrences. The arthropod communities were diverse and included detritivores and predators, though surprisingly few, if any, herbivores. This suggests that terrestrial arthropod assemblages were diversifying and increasing in complexity at the same time as terrestrial plants. The best-known lower Middle Devonian locality is the Rynie Chert of Scotland (Siegenian age; Rolfe 1980), which is complemented by the one-stage-younger Alken an der Mosel locality of Germany (Emsian age; Stormer 1970), and an upper Middle Devonian site from Gilboa of New York state (Givetian age; Shear et al. 1984).

The major interaction between plants and animals at this time was through detritus feeding, as deduced from animal morphologies, coprolite distributions, and the nature of plant damage. Although limited evidence has been adduced from damage repair to plants to support the existence of arthropod herbivory in the Early Devonian (Banks 1981; Kevan et al. 1975), it is not clear that such damage reflects systematic herbivory rather than misplaced detritivory. A number of detritus feeders are known, although they are not the dominants in species diversity or numbers of individuals at any of the best-studied sites. Millipeds appear to have been abundant throughout the Devonian (Almond 1985), although it is difficult to convert this abundance to a measure of ecological importance. Small arthropleurids are known from Alken an der Mosel (Størmer 1976) and Gilboa (Shear, unpublished data), whereas collembolans (springtails), which are very important soil and detritus feeders today, are reported in the Devonian only from the Rhynie Chert (Greenslade and Whalley 1986). Mites occur at Rhynie and Gilboa (Kethley et al. 1989); six species represent two major groups (orbatids and endeostigmatids) in the latter fauna. The earliest insects are archeognathans (machilid-like insects) from the Early Devonian of the Gaspé peninsula, Canada (Labandeira et al. 1988). Insect fossils are rare throughout the Devonian (Shear et al. 1984).

Numerically the most abundant animals at Rhynie and Gilboa are predators. This excess of predators, recorded consistently from the few Devonian localities known, persisted until the Late Carboniferous. The most important of these predators are the trigonotarbid arachnids, which are dominant numerically at Rhynie and are both dominant and diverse (9 species, more than 3 genera; Shear et al. 1987) at Gilboa. The earliest evidence of spiders (1 species), and silk production, comes from the Gilboa assemblage (Shear et al. 1989), which also includes other predators, such as centipeds (possibly 2 species), scorpions, and pseudoscorpions.

The earlier Devonian animal community is distinct from all post-Devonian assemblages. The dominance of predatory forms raises the question of how energy entered animal food webs and suggests a substantial bias. The pattern is noteworthy, however, because a predominance of predators similarly characterizes Carboniferous and Early Permian terrestrial tetrapod assemblages.

4.3 Synthesis

There were no directly reciprocal interactions between early plant and animal assemblages. Plant primary productivity clearly supported the animal food webs, but only through a detritus chain and not through herbivory. Detritivores contributed to soil development and nutrient cycling, which would have provided feedback to the plant communities. Plants, through their effects on resource accessibility and by moderating thermal extremes and providing protection from desiccation and predation, contributed to the patchiness and diversity of habitats. Through these effects plants created microhabitat variation and opportunities for specialization and evolutionary diversification of the animals (Rolfe 1985b). In general the system was integrated weakly, with animals as "epibionts" on the plant community. Dynamic interactions appear to have been confined mostly to plant-plant or animal-animal subsystems.

Plant communities of the Early and Middle Devonian had relatively high guild depth (the number of different species with similar ecological strategies and resource requirements). Plant species were morphologically stereotyped, mostly clonal space occupiers, lacking leaves and roots or with very small leaves and limited root systems. Although microhabitat specialization may have existed, entire groups of species probably had similar preferences. However, morphology alone suggests some differences in strategy among these plants. For example, *Rhynia gwynne-vaughnii* was probably a colonizing species (Diane Edwards 1980); deciduous branches may have allowed rapid dispersal across exposed or disturbed substrates. In contrast, *Aglaophyton* (previously *Rhynia*) *major*, a site-occupying form (Edwards 1986), had a typical clonal growth habit and probably "turfed in" in more physically stable environments. Both species occur in the Rhynie Chert.

The known aspects of morphology and environment suggest that the structure of early plant communities was controlled largely by the ability of plants to locate patches opened for colonization by disturbance or aggradation and by the ability of clones to exclude competitors through rapid space occupation or to escape competition or disturbance by rapid completion of the life cycle. On an ecological time scale, such ecosystems probably had very high structural stability, since many species had similar growth forms and life histories and could substitute for each other. If we use the terms defined by Pimm (1984), early Devonian plant communities were stable, low in species richness, and in a general sense, low in connectance (there were few interspecific interactions). The basic structural organization and dynamics should have remained the same in the face of all but the most severe and widespread perturbations, even if certain taxa disappeared or dominance-diversity patterns changed.

On a geological time scale (millions of years) such systems probably had low resistance, in the sense that the low connectance among the component taxa permitted incursions of new, more structurally complex plants. During the Devonian there were global directional increases in the structural complexity of plant communities. This is reflected both by increasing species richness (Niklas et al. 1980; Knoll 1986) and by the continuous morphological modernization of the flora (Chaloner and Sheerin 1979). At current levels of stratigraphic resolution, these increases appear to be continuous and relatively gradual. The early assemblages, composed of plants with primitive morphologies, were far from the biomechanical limits that could have been attained, given the constraints of tissues and developmental biology. The appearance of "biomechanically superior" plants (Knoll and Niklas 1987), which were taller and which had some combination of central root systems, leaves, seeds, and other less conspicuous features, initiated the displacement of the older species and the communities they formed, possibly through interspecific competition (Knoll 1984). Comparable generalizations can be drawn from the terrestrial invertebrate record of the Devonian, in which species richness and diversity of morphological specializations increase through time.

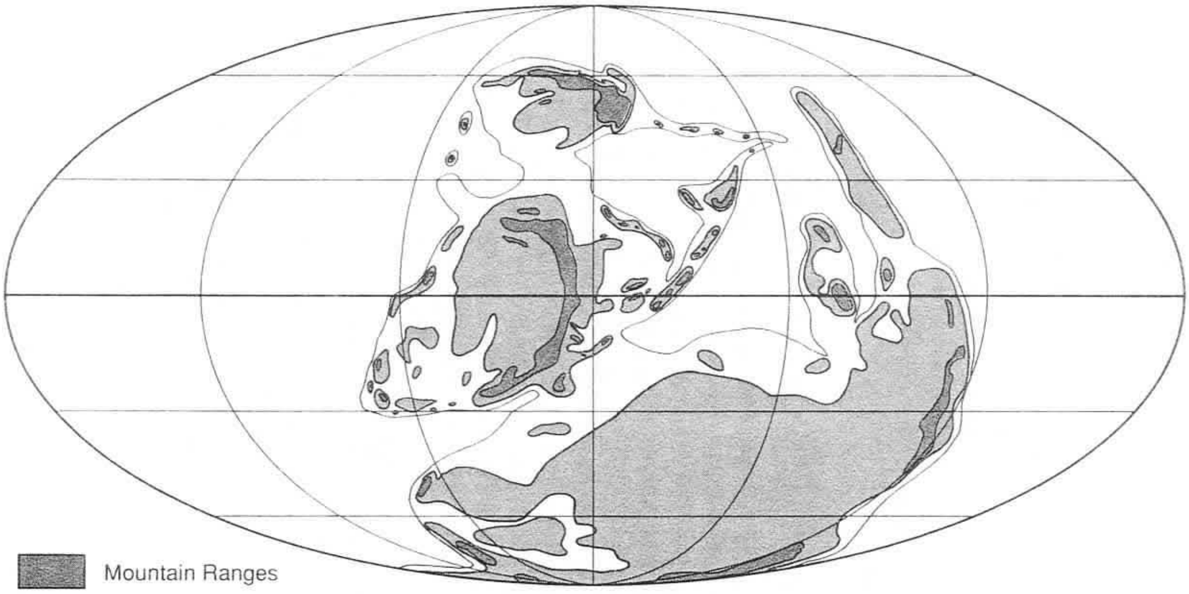
5 THE LATE DEVONIAN TO EARLY CARBONIFEROUS

Diversity, structural complexity, and biogeographic variability of ecosystems increased throughout the Devonian, and ecosystems developed some modern aspects by the Late Devonian and Early Carboniferous (Raymond 1985; Scheckler 1986a). During this time interval, modernization of animal-plant interaction and of animal trophic relationships appears to have lagged behind that of plant community structure (Beerbower 1985).

Fossil deposits of the Late Devonian and Early Carboniferous range from tropical to temperate paleolatitudes (Raymond 1985; Ziegler et al. 1981) (figure 5.3). On the basis of the degree of phytogeographic differentiation and the inferred changes in continental configuration during the Early Carboniferous, Raymond et al. (1985b) and Raymond (1985) infer climatic amelioration, trending toward warmer and wetter conditions throughout the period. In general, climate during the later Devonian and earliest Carboniferous in the Old Red Sandstone portion of Euramerica appears to have been warm and seasonally dry (Woodrow et al. 1973; Allen 1979). Studies of plant megafossils (Rowley et al. 1985; Raymond 1985; Raymond et al. 1985b) and microfossils (Zwan 1981; Clayton 1985) suggest three major phytogeographic subunits during this period, with the largest—the equatorial midlatitudes—further subdivided latitudinally.

An extinction in the Late Devonian had a major impact on plant communities and provides the earliest opportunity for study of plant community dynamics following a major species turnover. The first evidence of this extinction was found in the record of marine invertebrates at the Frasnian-Famennian boundary (McLaren 1982, 1983). Allowing for the vagaries of correlating marine and continental sections, biotic changes appear to occur earlier in terrestrial deposits, first among plants (Scheckler 1986a) and somewhat later among freshwater invertebrates (McGhee 1982).

LATE DEVONIAN (363 Ma)



- ▩ Mountain Ranges
- ▨ Lowlands
- ☐ Continental Shelf

Paleotopography

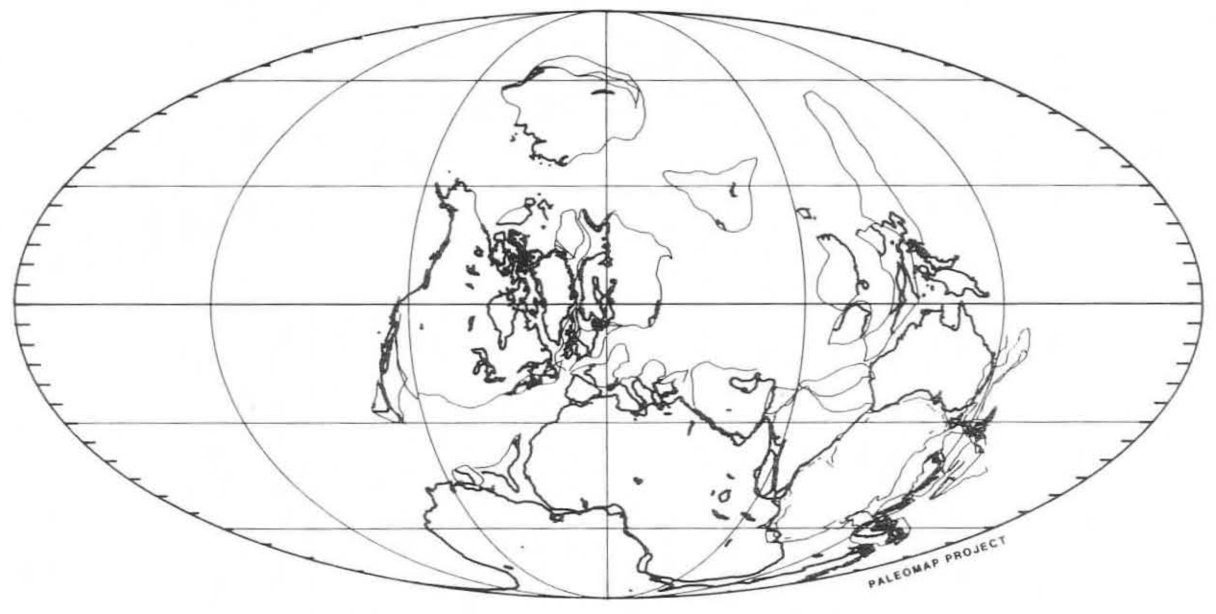


Fig. 5.3. Generalized continental positions and orography in the Late Devonian. (Courtesy of C. R. Scotese and the PaleoMap Project, University of Texas, Arlington.)

5.1 Plants

Late Devonian

Early Frasnian plant assemblages from New York state (Scheckler 1986c) are diverse and well known, but their paleoecology has not been assessed in detail. These plants are described briefly in order to provide a counterpoint to the postextinction late Frasnian floras, which are better understood paleoecologically.

The oldest Frasnian floras were dominated in terms of biomass by aneurophytalean progymnosperms, bushy shrubs to small trees. A few species of the progymnosperm *Archaeopteris*, large trees with trunk diameters up to 1 m, made their first appearance at this time, but in low abundances (Banks 1966, 1980; Scheckler 1986a). Many other kinds of plants were present, including early fernlike cladoxylaleans, Iridopteridales, and both herbaceous-trailing and arborescent lycopsids. In many constituents, these floras reflect ties to Middle and even Early Devonian floras.

During the middle of the Frasnian, significant floristic changes appear to have occurred, but the extent to which these changes reflect differences in the depositional settings is unclear. Aneurophytalean progymnosperms declined precipitously in abundance, and diversity drops from six to two genera in the New York section. Archaeopterid progymnosperms increased in abundance and diversity. Herbaceous "ferns" and lycopsids became rare to absent, although lycopsid trees remained. The landscape was altered drastically by the subsequent rise of *Archaeopteris* forests. These dominance-diversity changes have been attributed to the same factors that ultimately caused the Frasnian-Famennian marine extinctions (Scheckler 1986a), possibly climatic change associated with the onset of Gondwanan glaciation (Veevers and Powell 1987; Crowley and North 1988). The decline in diversity and major shifts in dominance patterns continued into the late Frasnian.

Late Frasnian plant communities also are known from localities in New York (Scheckler 1986a). The most characteristic plants are *Archaeopteris* species, some of which produced growth rings indicating some kind of seasonality (Creber and Chaloner 1984). Because nearly all species had small laminar leaves arrayed on large, flattened branch systems, a shaded forest was likely. These trees appear to have produced many deciduous branches with attached laminate foliage, which resulted in a much greater yield of litter than that produced by earlier plants; the branches may have been shed seasonally, perhaps at the beginning of the dry season (Scheckler 1978). Increased amounts of litter may have accentuated the role of fire in these communities as a factor in disturbance and succession (Cope and Chaloner 1980; Chaloner and Cope 1982; but see also Beck et al. 1982). *Archaeopteris* trees formed low-diversity gallery forests in waterlogged soils along streamsides or on wet floodplains, as suggested by abundant *Archaeopteris* remains in channel and organic-rich sediments (Beck 1964; Retallack 1985a, b). Late Frasnian calcareous paleosols have been interpreted as well-drained areas that may have supported shrubby and herbaceous vegetation (Retallack 1985a). Such landscapes probably had considerable spatial heterogeneity, which is more detectable with paleosols than with the limited spectrum of environments that preserve megafossils.

Forested areas had become common by the late Frasnian and there were clear habitat distinctions among the plants. Structural and taxonomic diversity, although low, were increased relative to earlier Devonian plant communities. However, guild depths of trees in many of these environments were low, with limited overlap in any one assemblage. This should have predisposed these ecosystems to extensive structural change in the face of extinctions.

Throughout the Famennian, diversity and structural complexity of plant communities increased, both within and between habitats. Lowland nearshore vegetation appears to have been differentiated into a number of discrete types composed of shrubby colonizers, forest trees, ground cover, vines, and stress-tolerant swamp specialists. This is demonstrated by studies of Famennian deposits from the eastern United States, southwestern Ireland, and Arctic Norway. In the Famennian of Virginia and West Virginia (Scheckler 1986b), the first peat swamps have been identified and are clearly segregated taxonomically from floodplain forests, which contain the earliest evidence of seed plants (Scheckler 1986b; Gillespie et al. 1981). Peat swamps from this area were nearly monodominant stands of the fern *Rhacophyton*. These floras occur at four spatially and temporally distinct localities in fluvial channel-fill and coastal peat deposits. In addition to *Rhacophyton*, they contain minor amounts of apparently allochthonous debris from aborescent lycopsids that grew in swampy areas fringing the peat deposits (Beeler and Scheckler 1983). By the Early Carboniferous, these lycopsids were the dominant elements of peat-forming swamps, a position they occupied until the Stephanian in Euramerica (Phillips et al. 1974; Scheckler 1986c).

Famennian forests in non-peat-accumulating, lowland environments of Virginia and West Virginia were dominated by a mixture of *Rhacophyton ceratangium* and three species of *Archaeopteris* (*A. halliana*, *A. macilenta*, *A. hibernica*). Although these sites appear to have been better drained than the coexisting swamps (Scheckler 1986b), floodplain paleosols suggest relatively wet conditions (Retallack 1985a).

A still-greater diversity in lowland habitats is suggested by storm deposits that also contain linguloid brachiopods and fish (Scheckler 1986b). The dominant elements in these deposits are *Rhacophyton ceratangium* (40% of the vegetation) and up to five species of *Archaeopteris* (three above, as well as *A. obtusa* and *A. sphenophyllifolia*; an additional 40% of the biomass). The remaining 20% of the biomass is divided among lycopsids, seed plants, and ground cover, such as *Sphenophyllum subtenerrimum*. Although these plants are allochthonous, they record a structurally and taxonomically diverse vegetation that existed in wetlands surrounding the peat swamps. Seed plants in these deposits may have been colonizers, because they appear to have been small and produced small seeds (4 to 5 mm in diameter).

A general picture of the latest Devonian plant communities comes from deposits in Arctic Norway that demonstrate the control of floristic heterogeneity largely by physical factors (Scheckler 1985, 1986a; Fairon-Demaret 1986; Kaiser 1970). Work on this flora is in progress, but four major habitats appear to be represented. Peat-forming wetlands, preserved as coals or organic-rich shales, were dominated by a lycopsid tree, *Cyclostigma*. This genus had a stigmarian-like root system and is the earliest evidence of such lycopsid trees in peat swamps. Streamside habitats, represented by clastic rocks overlying the coals and in overbank deposits, were dominated by the clonal *Pseudobornea*, a putative calamite precursor. Poorly drained soils supported a low-diversity forest of large *Archaeopteris hibernica* trees. In better-drained areas of floodplains, the dominant tree was *Archaeopteris fimbriata*, a tree smaller than *A. hibernica;* this forest was patchy, with *Rhacophyton ceratangium* being either a local dominant or part of an understory along with *Sphenophyllum*.

A very different picture is presented by latest Devonian floras from southwestern Ireland (Matten et al. 1984; Matten et al. 1980a; Matten et al. 1980b). Integration of the vegetational patterns with depositional environments (Bridge et al. 1980) indicates that the flora was dominated by seed plants, probably of the "seed fern" groups Calymopityaceae and Lyginopteridaceae, which makes this the oldest-known seed-plant dominated vegetation. These assemblages occur in floodplain sequences that include soils with well-developed nodular carbonate beds indicative of well-drained conditions and low sedimentation rates on the floodplain. The small stature of the vegetation and its reproductive attributes suggest r-selected plants adapted to periodic environmental disturbance, probably by flooding. Such a habitat would have been more conducive to seed-plant dominance than to dominance by lower vascular plants; the larger lower vascular plants would have required more extended periods of undisturbed, predictably wet conditions.

These three floras demonstrate that vegetational patterns strongly reflected physical habitat variability by the end of the Devonian. A wide range of ecological strategies is seen in the plants; most of them also have distinct preferences for specific environmental conditions. At opposite ends of the ecological spectrum are well-drained habitats, newly accessible to seed plants because of their ability to reproduce without the need of water, and the long-inhabited wetlands. Vegetation of Late Devonian (Famennian) peat-accumulating wetlands (*Rhacophyton*-dominated) and similar environments of the Early Carboniferous (Tournaisian) (*Lepidodendropsis*-dominated) contain just one species each (Scheckler and Beeler 1984; Scheckler 1985, 1986a, 1986b, 1986c). Similar monospecific dominance, by an early gymnosperm, is found in pioneer dry habitats in the Late Devonian (Famennian) (Rothwell and Scheckler 1988). Wetlands, however, seem to differ from other settings in that they were apparently not areas of taxonomic innovation. Rather, as demonstrated by the examples discussed below, the wetlands became refugia for relict plants (Knoll, 1985; DiMichele et al. 1987).

Diversification of early gymnosperms may have occurred in the absence of interspecific competition for habitat space (Rothwell and Scheckler 1988; DiMichele et al. 1989). Early gymnosperms prospered less by successful competition than by rapid exploitation of a previously unused habitat, such as primary successional areas on a prograding delta margin. This pattern of seed-plant dominance in nonswamp habitats was to characterize the Carboniferous. However, many small lower vascular plants accompanied seed plants in the drier floodplain environments of the Devonian.

Early Carboniferous

Early Carboniferous plant assemblages, although known from a relatively small number of localities, occur worldwide (Raymond et al. 1985b; Raymond 1985). There are major differences between Late Devonian and Early Carboniferous floras and their vegetational structures, and these are reflected in major changes in dominance-diversity patterns. Because both *Archaeopteris* and *Rhacophyton* were extinct by the Early Carboniferous, Tournaisian (basal Carboniferous; see fig. 5.1) landscapes were markedly different. Areas that were forest dominated for the previous 15 million years gave way to an entirely new plant-community organization. No tree-sized counterparts of *Archaeopteris* capable of forming dense, shady forests are known prior to the end of the Tournaisian and beginning of the Visean, when the gymnosperm *Pitus* appears (Scott 1988; Retallack and Dilcher 1988). The remaining vegetation, including newly evolved forms growing in floodplains and other lowland environments, appears to have been enriched in species more to the r-selected end of the life-history spectrum; these were largely shrubby pteridosperms, less than 2 m in height. Swamp floras continued to be taxonomically distinct from contemporaneous floodplain vegetation, and some swamps were dominated by trees, mostly midsized tree lycopsids (Scheckler 1986a). The physicochemical attributes of swamp environments may have buffered these habitats from many of the perturbations that affected other lowland vegetation, imparting a degree of taxonomic and vegetational conservatism (Knoll 1986; DiMichele et al. 1985, 1987).

Reports of Early Carboniferous plant assemblages from the Tournaisian and Visean indicate significant regional diversification and further development of the ecological distinctions suggested by the latest Devonian floras (see summaries in Scott et al. 1984; Scheckler 1986a; Scott and Rex 1987; Bateman and Rothwell 1990). Among Early Carboniferous floras, those from the late Tournaisian have received the most detailed paleoecological study.

Within a deltaic, coal-bearing sequence of Virginia (Scheckler and Beeler 1984; Scheckler 1986a, c), the lycopsid tree *Lepidodendropsis* dominated coastal swamps of lagoonal or back-barrier settings, as well as floodplain swamps. Calamite trees or shrubs (*Archaeocalamites*) were common in stream-margin environments, whereas better-drained habitats were dominated by ferns and pteridosperms, such as *Neurocardiocarpus* on levees and *Triphyllopteris* and *Rhodeopteridium* in drier interdistributary areas. This basic subdivision of lycopsid abundance in peat and some clastic swamps, pteridosperm dominance of better-drained habitats (presumably levees and floodplains), and local sphenopsid abundance in disturbed or stream-margin environments is typical of the Late Carboniferous (Oshurkova 1974; Scott 1978; Pfefferkorn and Thomson 1982) and appears to have been established by the late Tournaisian. Notwithstanding these generalizations, distributions of the major plant groups overlapped broadly within lowland areas.

A different suite of environments within volcanigenic terrains is known from numerous late Tournaisian and Visean exposures in western Europe (Scott et al. 1984; Rowe and Galtier 1989). Despite the volcanic overprint, the basic partitioning of ecological resources and habitats by the major plant groups appears to be the same as the partitioning identified in the roughly coeval coal-bearing sequence of Virginia (Scheckler 1986a). The floras are preserved in a variety of coastal-lowland paleoenvironments, ranging from lakes and small swamps in which muddy peat accumulated to disturbed areas that were subject to periodic volcanic ash falls and debris flows (Rex 1986; Bateman and Scott 1990). The general climate of the regions in which the plant-bearing deposits were formed appears to have been seasonally wet, perhaps within an area of monsoonal circulation and occasionally heavy rainfall (Bateman and Scott 1990). These environments present a strong contrast to those that characterize Upper Carboniferous coal-bearing sequences, where poor drainage, increased equability of rainfall, and reduced levels of disturbance permitted development of regionally extensive, relatively homogeneous floras of tree-sized plants (Pfefferkorn and Thomson 1982). The volcanigenic floras of the Early Carboniferous suggest that disturbed, moisture-limited environments existed during times of increased lowland floral homogeneity, such as in the Late Carboniferous, but are not preserved. The floras of Lower Carboniferous deltaic lowlands (Scheckler 1986a, c) appear to be linked more closely to Late Carboniferous coastal and deltaic lowland floras than do Lower Carboniferous floras from volcanigenic lowlands.

The most completely studied Tournaisian plant assemblage is that of Oxroad Bay in Scotland (Scott et al. 1984, 1985b; Bateman and Scott 1990; Bateman and Rothwell 1990). This assemblage is drawn from many plant-bearing horizons from a variety of depositional environments. It is a microcosm of the physical heterogeneity that appears to characterize all the Lower Carboniferous sites of western Europe. A general picture emerges of local variability in floristic composition that was controlled largely by physical conditions. In the wettest parts of floodplains, the lycopsid tree *Lepidodendron calamopsoides* and the pteridosperm *Stenomyelon tuedianum* formed the dominant canopy vegetation (Scott and Rex 1987), while the more disturbed parts of the wetter habitats were dominated by the scrambling, ground-cover lycopsid *Oxroadia* and other lower vascular plants, including calamites and some ferns. The major plant groups that dominated these wetter environments, even within the disturbed areas, were basically the same as those from more uniformly wet, deltaic lowlands, but the species and generic composition was generally very different. Pteridosperms, particularly those with r-selected life histories (small stature, small seeds, high reproductive output), formed an open vegetation in areas that were more heavily disturbed by volcanic activity and that were subject to water deficits (Rothwell and Scott 1985). This type of flora varies greatly from site to site and is distinct from floras of coastal wetlands.

Another putatively Tournaisian flora (possibly early Visean: R. Bateman pers. comm. 1991) is the "lower flora" from Loch Humphrey Burn, Scotland, which is dominated by ferns. A large proportion of these ferns are fusinized (preserved as charcoal), which leads Scott et al. (1985b) to suggest that ferns were colonizing volcanigenic areas that were subject to fires; the early radiation of ferns may have occurred in these environments during the Lower Carboniferous (Scott and Galtier 1985; Galtier and Scott 1985). Possibly the most significant observation about these floras is that they contain numerous taxa not recorded from any Tournaisian nonvolcanic settings, implying further habitat and biogeogragraphic subdivision among the pteridosperms and ferns of nonswamp environments.

Late Visean floras from volcanigenic terrains show similar vegetational patterns to those of the Tournaisian, despite the addition of many new species (Scott 1990). Floras and depositional environments have been described from a number of sites, including Kingswood (Scott et al. 1986), Pettycur (Rex and Scott 1987; Scott and Rex 1987), Loch Humphrey Burn (upper flora: Scott et al. 1984), and East Kirkton (Rolfe et al. 1990), in Scotland, and Esnost (Rex 1986) in France. Although the range of depositional environments represented at some of these localities is similar (Kingswood, Pettycur, and the upper Loch Humphrey Burn beds are disturbed volcanigenic landscapes with local lakes or peaty mud deposits), they have very few taxa in common (Scott et al. 1986; Bateman and Rothwell 1990). A comparison of Kingswood with the several localities at Pettycur (Scott et al. 1986) suggests a complex vegetational mosaic. Open lakes were fringed by a vegetation of herbaceous lycopsids with some gymnosperms of indeterminate affinities. Surrounding these lakes were better-drained areas subject to frequent fires. Such disturbances favored weedy seed plants, particularly pteridosperms, which were diverse at the Kingswood locality. On poorly drained, weathered lava surfaces, ferns occupied areas that were periodically burned. In these relatively disturbed volcanic areas, the most diverse vegetation is found in swamp deposits from Pettycur, which formed in depressions on lava-flow surfaces. Like most other Carboniferous localities, these swamps were dominated by lycopsid trees of several kinds, along with sphenopsids, filicalean ferns, and small pteridosperms (e.g., *Heterangium*).

These Tournaisian and Visean deposits demonstrate that the major plant groups had partitioned the land surface along distinct ecological lines. In particular there was a division between plant groups common in wetlands and those of better-drained habitats. The division was largely complete by the late Tournaisian. Within better-drained areas, pteridosperms and ferns were further subdivided, so that a vegetation composed largely of r-selected colonists dominated the most marginal habitats. The basic vegetational patterns seen in these deposits and the associations of higher taxa with particular habitats persisted until the end of the Carboniferous.

Diversification of species and plant architectures continued through the Early Carboniferous (Knoll et al. 1984; Niklas 1986). During this time all major taxonomic groups of vascular plants evolved: seed plants, ferns, sphenopsids, and several lycopsid groups. Relative to subsequent Phanerozoic plant radiations, it was an explosive, high-level taxonomic radiation (the angiosperms, although diverse, are still only a variation on the seed plant organizational theme). Accompanying this taxonomic diversification was an architectural diversification. Among the trees, major taxonomic groups appear to have had fundamentally different architectures, different basic ecological habitat preferences, and different life-history patterns. This led to a significant congruence between phylogenetic lineages of plants and ecological strategies, such that taxa of the same clade tended to have similar ecologies. This taxonomic and ecological overlap, which is unique to the Carboniferous, reached its zenith in the Westphalian (DiMichele et al. 1987).

Despite the taxonomic differences between the plants of the Carboniferous and those of later times, vegetation became structurally modern during this time, probably by the Visean (Scheckler 1986a). Canopy stratification developed. Lianas and possibly epiphytes became part of the vegetation. Spatial heterogeneity was great, and plants occupied and extended the diversity of basinal lowland habitats. Viewed from afar, the forests may not have looked too different from those of today, although taxonomic composition was totally different.

5.2 Animals

There are very few terrestrial animal assemblages known from the Late Devonian through the Early Carboniferous (Frasnian-Visean). Because better-known Late Carboniferous assemblages suggest continued importance of arthropods as the base of animal trophic relationships, such relationships are presumed to have prevailed in the Late Devonian and Early Carboniferous. Terrestrial vertebrates probably underwent major radiations during this time, but there is little direct evidence for this.

Arthropods

Detritivorous arthropods appear to have remained the major link between plants and animal food webs. Millipeds are present in Devonian to Upper Carboniferous rocks (Almond 1985; Hannibal and Feldmann 1981), minute arthropleurids first appear in the Middle Devonian (Shear 1986), and gigantic arthropleurids up to 2 m long are present in Upper Carboniferous deposits (Rolfe and Ingham 1967; Hahn et al. 1986). Mites and collembolans (springtails) first appear in the fossil record in the Early Devonian, and although they are unrecorded by body fossils in the Late Devonian and throughout the Carboniferous, they undoubtedly were present. In addition to these major detritivorous groups, many early litter-reducing insects (e.g., blattoids), though not found as fossils in Upper Devonian and Lower Carboniferous rocks, were probably in existence.

Scorpions, centipeds, and several orders of arachnids were, by inference, major predators during the Early Carboniferous, although body fossils of these groups are rare. Documentation of their presence may soon be forthcoming from the Lower Carboniferous of Scotland (Wood et al. 1985).

A diversity of winged insects is known from Namurian rocks (Wooten 1981), suggesting an earlier diversification. Certain protorthopteroids had biting mouthparts and mantislike front legs and may have been predators of other insects (Carpenter 1971; Burnham 1983). Grasshopper-like forms with biting mouthparts (Sharov 1968) also were present and may have been herbivorous. The majority of Late Carboniferous winged insects had mouthparts apparently adapted for pulling apart plant reproductive organs and sucking up the contents, suggesting that herbivory may have been established in the less-well-known Namurian record (see §6.2). At present it is not possible to estimate the extent of arthropod biomass supported by herbivory. However, changes in plant structure, particularly hardened, sclerotic seed coats and increased abundance of tough sclerenchyma in pollen organs and stems, suggest that by the beginning of the Namurian, herbivorous insects had become a significant selective factor.

Vertebrates

Evidence of terrestial vertebrates in the Devonian is sparse but geographically widespread. In addition to amphibian trackways from Australia (Warren and Wakefield 1972) and questionable footprints from Brazil (Leonardi 1983), the first amphibian fossils come from the uppermost Devonian of East Greenland and Russia (Jarvik 1952; Milner et al. 1986; Clack 1988, 1989; Coates and

Clack 1990). These include ichthyostegid and anthracosaurian amphibians, which probably preyed on arthropods or aquatic animals.

There are about ten Lower Carboniferous (mostly Visean) tetrapod-bearing deposits known from Scotland and eastern North America. With few exceptions, these deposits also contain freshwater fishes and may be regarded, in a colloquial sense, as lake assemblages (Smithson 1985a; Milner et al. 1986). These assemblages are dominated by a variety of aquatic to semiaquatic tetrapods. A recently rediscovered Visean-age deposit near East Kirkton, Scotland (Wood et al. 1985; Rolfe et al. 1990) has a fully terrestrial tetrapod biota that indicates a greater degree of tetrapod adaptation to the terrestrial environment than previously known.

Despite a predominance of amphibious-to-fully-aquatic amphibians in Devonian and Lower Carboniferous deposits, a diversity of terrestrial forms has been recognized, all of which were insectivorous or carnivorous (table 5.1).

1. Ichthyostegalians. *Ichthyostega*, known only from the Devonian of East Greenland, was approximately a meter in length. Its stout forelimbs were certainly capable of terrestrial locomotion, but other characteristics suggest a more amphibious habit (Jarvik 1952, 1980). The appendicular skeleton of *Acanthostega* indicates an aquatic mode of life (Coates and Clack 1990).

2. Anthracosaurs. Postcranial remains from the Devonian of Russia have been ascribed to a new proterogyrinid anthracosaur (Lebedev 1984). Complete proterogyrinid skeletons from the Visean of Iowa, Scotland, and West Virginia represent amphibians about 0.5 to 1.5 m in length (Holmes 1984; Milner et al. 1986; Bolt et al. 1988). Although these short-bodied forms had substantial limbs (Holmes 1980), their somewhat reduced forelimbs, which lacked well-ossified carpals, and dorsoventrally expanded tail suggest that they were amphibious predators. Proterogyrinids are accompanied by comparably sized eoherpetontid anthracosaurs in Lower Carboniferous deposits. With jaw architectures for feeding on land and massive limbs, *Eoherpeton* is interpreted as a terrestrial predator (Smithson 1985b).

3. Temnospondyls. Discoveries from East Kirkton include at least two types of intermediate-sized (30 to 50 cm in length) terrestrial amphibians that resemble the lower Westphalian temnospondyl *Dendrerpeton* (Wood et al.

Table 5.1 Lower Carboniferous (Visean) Terrestrial Amphibians

	Small	Large
Carnivores		Proterogyrinid anthracosaurs Eoherpetontid anthracosaurs
Insectivores	Aïstopods? "Dendrerpetontid" temnospondyls	

Note: Size categories are based on estimated total body lengths of largest specimens (not applicable to aïstopods), small < 0.5 m, large ≥ 0.5 (but generally less than 1.5 m)

1985; Milner et al. 1986). These forms were somewhat froglike, with large orbits, short snouts, relatively open palates, short presacral columns, and well-ossified limbs. Large posteriorly facing emarginations at the skull table–cheek junction, generally termed otic notches, may have supported tympanic membranes capable of transmitting air-borne sounds to the inner ear. Although further study is necessary to confirm details of otic structures, such sensory adaptations would have facilitated an active terrestrial existence.

Isolated remains of rhachitomous amphibians and trackways bearing forefoot imprints with four digits indicate the existence of other, presumably terrestrial, Early Carboniferous temnospondyls that exceeded a meter in length.

4. Aïstopods. Because of their aberrant morphology and widespread occurrence, the life habits of aïstopod amphibians are difficult to assess. These snakelike amphibians lacked limbs and girdles and occur in fish-dominated as well as non-fish-bearing assemblages throughout the Carboniferous (Wellstead 1982; Milner et al. 1986). Cranial and dental specializations within the group indicate dietary preferences for either soft- or hard-bodied prey. A complete, fully ossified specimen measuring approximately 30 mm in length suggests further that aïstopods may have been characterized by direct development without an obviously aquatic larval stage (Baird 1965). Although most authors regard the group as aquatic, some aïstopods may have thrived in non-aquatic settings.

5. Amniotes. A virtually complete amniote skeleton in the Visean-age East Kirkton deposit provides further evidence of a taxonomically diverse terrestrial fauna in the Early Carboniferous. Authoritatively identified as an amniote on the basis of the skull-roof pattern and tarsal configuration (Smithson 1989), this specimen also has the long, lightly built limbs of a highly terrestrial form. Further ecological inference and taxonomic assignment await detailed description.

Because most tetrapod-bearing deposits represent wetland or lowland areas, tetrapods of this time have been considered to be strongly linked to the aquatic environment for food and reproduction. However, glimpses of a fully terrestrial fauna such as that provided by the East Kirkton site and the appearance of terrestrial forms within nearly all major tetrapod groups by the end of the Westphalian belie the traditional picture of a solely water-based Early Carboniferous terrestrial fauna. It appears likely that just as plants and arthropods were moving rapidly and adaptively into a broad spectrum of habitats, so were vertebrates.

5.3 Synthesis

Throughout the Late Devonian and most of the Early Carboniferous, the major linkage between animal food webs and primary plant productivity appears to have been the detritivorous arthropods. Insect herbivory, which may have appeared before the Namurian, altered considerably the selective environment for plants and favored structural and biochemical defenses. It is difficult to demonstrate a direct response to insect predation pressures because of the complex interaction of plants with many aspects of their environment and the possibility of the random fixation of traits during the early radiation of plant lineages. As indirect, and certainly equivocal, evidence of the effects of predation, stony seed coats and other potentially protective seed-coat complexities appeared; seeds with open integuments were less common by the Namurian. Successful pteridosperm (Medullosaceae and Lyginopteridaceae) radiations in drier habitats may in part reflect the presence of tissues enriched in resinlike substances and cortical sclerenchyma, both of which could have deterred insect predation. The expansion of insect herbivory would have introduced a strong modifier on plant-plant interspecific and intraspecific interaction and would have expanded the resource base for insectivores. Insect herbivory provides the potential for significantly more integration of the plant and animal components of the ecosystem, including the potential for a negative feedback between plants and animals due to the direct effects of natural selection. Extensive herbivory should have had a strong influence on plant structure and life history and may have altered ecosystems in ways that we may be unable to detect at a cause-effect level.

Plant community structure and dynamics during this time had increased in complexity over the earlier Devonian. During the Late Devonian, habitat or niche partitioning appears to have been well established. Guild depth, however, was low. The ecomorphotype-to-species ratio would have been very close to one. As a consequence the options for successional recovery were few. Over short time spans (thousands of years) such systems may have been relatively stable with higher levels of species-species connectedness because of greater species resource specificity than in earlier Devonian ecosystems. Local and regional patterns of disturbance and recovery may have been comparable in their degree of regularity to modern systems in similar physical settings. However, over millions of years the low guild depth should have made these communities very susceptible to dramatic changes in both dominance-diversity hierarchy and structure. This may be reflected best by the disappearance of *Archaeopteris* forest trees at the end of the Devonian. With this change, the canopy in the wetter parts of many floodplain areas went from many meters in height to perhaps 2 m or less. Structural and ecomorphic recovery from these kinds of events appears to have occurred on a time scale of millions of years.

In contrast to earlier assemblages, Late Devonian and especially Early Carboniferous plant communities may have been more resistent to invasion by "biomechanically superior" forms (*sensu* Knoll and Niklas 1987). High levels of resource partitioning are indicated by the environmental restrictions of many plants. For example, the abundance and diversity of lycopsid trees was centered in wetlands, particularly swamps, from near the beginning of the Early Carboniferous to the later part of the Late Carboniferous. The lycopsid trees were replaced as dominants in wetlands by ferns and pteridosperms only after extrinsically induced extinctions (Phillips and Peppers 1984). Less dramatic examples can be provided for the ecological roles and physical distribution of sphenopsids, ferns, and progymnosperms. In essence, once an ecological resource space was occupied by biologically complex plant groups the likelihood of further invasion or partitioning of that resource space by other groups declined; these data appear to support the tessera model of Valentine (1980). Changes in the habitat breadth of major lineages, and hence the ecological status quo, appear to be linked to extinction of earlier occupants and the creation of broad resource voids by extrinsic physical disruption rather than by biotic competition (see theoretical discussions in Valentine 1980; Vermeij 1987; Erwin et al. 1987; Valentine and Walker 1987).

The Late Devonian and Early Carboniferous saw the establishment of ecosystems with potential for persistence over time intervals of millions of years. What can be thought of as "ecological constraints" developed on the dynamics of the botanical part of terrestrial ecosystems. The established vegetational structure reflected a relatively high degree of convergence between ecomorphotypic and phylogenetic groups. This convergence means that most major clades had relatively narrow ranges of ecological tolerance; this restricted available habitat space for each clade and channeled subsequent plant evolution by strongly limiting the range of ecological opportunities open to novel phenotypes. The likelihood of occurrence and especially of the survival of new phenotypes was diminished as long as extinctions did not eliminate major clades in this ecotaxonomic landscape. Although this picture is simplified, it encapsulates the main threads of a pattern that was established in the Late Devonian and Early Carboniferous and persisted into the Permian.

The small number of Upper Devonian and Lower Carboniferous animal deposits limits our ability to gauge their temporal dynamics. The differences between Late Devonian and Late Carboniferous assemblages suggest that animal communities of the Early Carboniferous were developing rapidly. The basic ecomorphic structure of carnivore domination seen in Late Carboniferous vertebrate and arthropod assemblages seems to have been in place by the end of the Early Carboniferous. Only insect herbivory may have been a primary agent altering plant community structure and dynamics, which appear relatively modern well before modernization of the animal assemblages. Terrestrial tetrapods of the Early Carboniferous radiated into a landscape devoid of preexisting vertebrate competitors. The early vertebrate communities were unlike any that have existed since. In the absence of herbivores, and with the strong aquatic linkages of most of the known species, early tetrapods appear to have had little impact on plants during a time when many of the most basic attributes of plant communities were evolving.

6 THE LATE CARBONIFEROUS: WESTPHALIAN AND STEPHANIAN

The Westphalian was the zenith of peat formation in Euramerica, which was located in tropical latitudes during the Late Carboniferous. The beginning of the agglomeration of the continents into Pangaea during this time is thought to have affected patterns of air circulation and climate (Parrish 1982), which also may have been influenced by glaciation in southern Gondwana during the Westphalian and Stephanian (Crowell and Frakes 1975; Visser 1987, 1989; Veevers and Powell 1987). Although the details of continental configuration (fig. 5.4) and specific climatic inferences are debated, patterns of air circulation and associated rainfall and changes in latitudinal positions of the continents may have had a major impact on plant and animal distribution (DiMichele et al. 1987; Knoll 1984; Olson 1985b).

During this time, ecological dominance of lowland habitats was shared by more orders and classes of plants than at any time in earth history. Global vegetational provinces had developed: Euramerican vegetation, the best known, was distinct from that of Gondwana (southern hemisphere) and Angara (Siberia), and to some extent from that of Cathaysia (China) (Chaloner and Lacey 1973; Chaloner and Meyen 1973, Zhao and Wu 1979; Raymond et al. 1985b; Zhang et al. 1987; Laveine et al. 1987). In Euramerica, Angara, and Cathaysia, the dominant plant groups were lycopsids, cordaites, and pteridosperms, although there were marked differences in generic and specific composition. Gondwanan floras were distinct and apparently had little taxonomic exchange with the other regions (Archangelsky 1986).

Westphalian and Stephanian plants are probably the best known of the Paleozoic, if not the entire pre-Cretaceous, largely because of their preservation in coal-bearing strata. Similarly, Westphalian arthropods and tetrapods from peat-accumulating wetland environments are better known than those of the Devonian and Lower Carboniferous. Plants from better-drained habitats, or from lowland environments that were not sites of major peat accumulation, especially in western parts of North America, also are known from a few occurrences (e.g., Pepperburg 1910; Read 1934; Read and Merriam 1940; Arnold 1941; Mamay and Read 1956; Tidwell 1967, 1988; Tidwell et. al. 1974; Leary and Pfefferkorn 1977; Leary 1981; Ash and Tidwell 1982; Winston 1983; Rothwell and Mapes 1988), and demonstrate the existence of xeromorphic vegetation in areas proximate to the wetlands (Havlena 1970).

There were major changes in the taxonomic composition of lowland Euramerican vegetation from the Westphalian to the Stephanian. The arborescent lycopsids *Lepidodendron*, *Lepidophloios*, *Asolanus*, *Diaphorodendron*, *Anabathra*, and *Bothrodendron* have not been found in Stephanian-equivalent rocks of North America and are presumed to have been extirpated throughout most of this part of Euramerica (Phillips et al. 1974). *Sigillaria* survived in North America, and several other genera, notably *Lepidodendron*, *Lepi-*

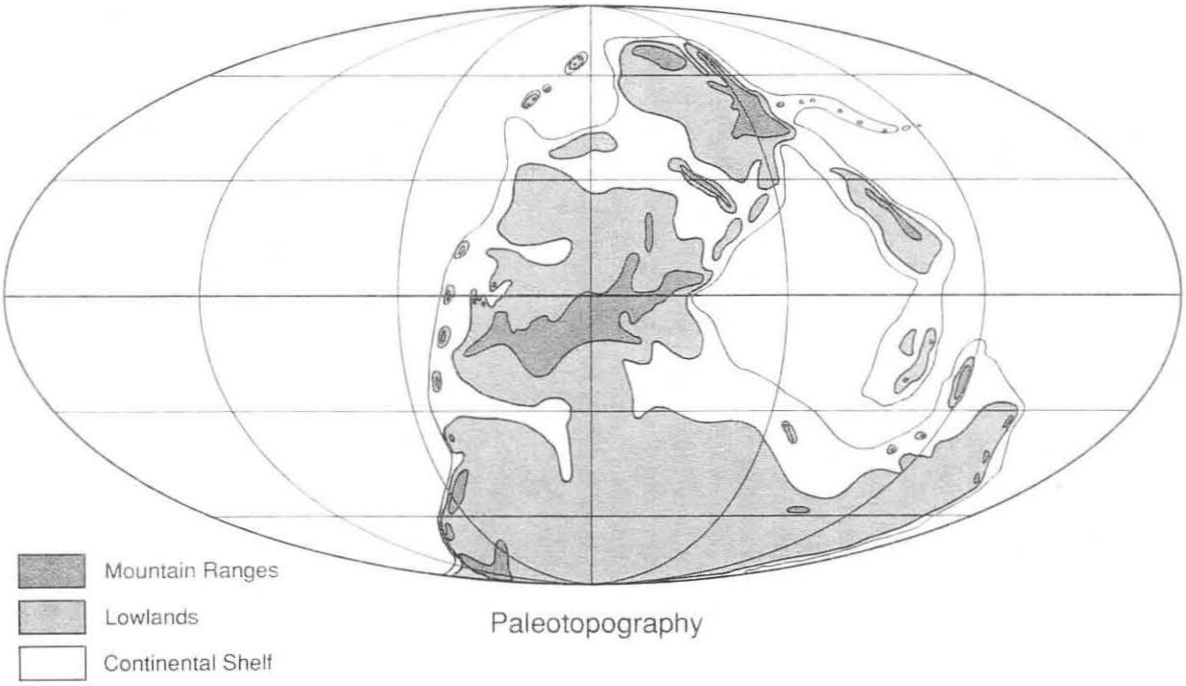
dophloios, and *Asolanus*, persisted in parts of southern and north-central Europe and in the Donets Basin of eastern Europe into the Stephanian (Stschegolev 1975; Boersma 1978; Lorenzo 1979; Kerp and Fichter 1985). Pteridosperms and tree ferns became the dominant elements of Stephanian lowland-wetland assemblages throughout Euramerica. As monographic research proceeds on ferns and pteridosperms, it appears that major taxonomic changes in these groups coincide with the changes in lycopsids (Mickle 1984; Lesnikowska 1989) throughout the wet lowlands (Phillips and Peppers 1984; Pfefferkorn and Thomas 1982), possibly because of increasingly dry or seasonal climate (Phillips and Peppers 1984; Cecil et al. 1984; Durden 1984a; Cecil and England 1989).

The Westphalian was the last Phanerozoic epoch to lack tetrapod herbivores. Although the diversity of amphibious and terrestrial tetrapods had increased, they remained insectivorous or carnivorous. The first tetrapod herbivores are thought to have evolved in the Stephanian within habitats that supported mesomorphic-to-xeromorphic plants. Arthropods, including flying insects, were diversified by the Late Carboniferous and appear to have had nearly as large a spectrum of ecological strategies as they do today: predators, detritivores, and herbivores were present, some with large body sizes. The substantial fossil record of arthropods suggests they had an important role in shaping the structure and dynamics of Westphalian and Stephanian plant communities (Labandeira 1990).

6.1 Plants

Upper Carboniferous plant assemblages are known from hundreds of localities in the Euramerican lowland wetlands. In contrast, comparatively little is known of floras from true upland environments (*sensu* Leary 1981), and there even has been speculation that higher elevations were not vegetated (Remy 1975). Westphalian vegetation can be divided broadly into that of wetland areas where peat formation occurred, and that of typically better-drained environments in which little or no peat accumulated. Within deltaic and coastal wetland environments, a more specific subdivision into peat-forming and non-peat-forming habitats is possible (Havlena 1970; Mapes and Gastaldo 1986). Transitional clastic swamp habitats supported vegetation intermediate between peat swamps and better-drained clastic soils. In overview it is clear that peat-forming and non-peat-forming habitats were edaphically distinct physical settings that supported different kinds of plant assemblages. During the Westphalian, when these distinctions were greatest, peat-forming habitats were dominated by several genera of lycopsid trees and, in some settings, by cordaitean gymnosperms (Phillips et al. 1985). Wetlands were otherwise dominated by pteridosperms, with increasing abundances of ferns late in the Westphalian (Pfefferkorn and Thomson 1982; see Collinson and Scott 1987b for a review of plant biologies and environments).

LATE CARBONIFEROUS (306 Ma)



Paleotopography

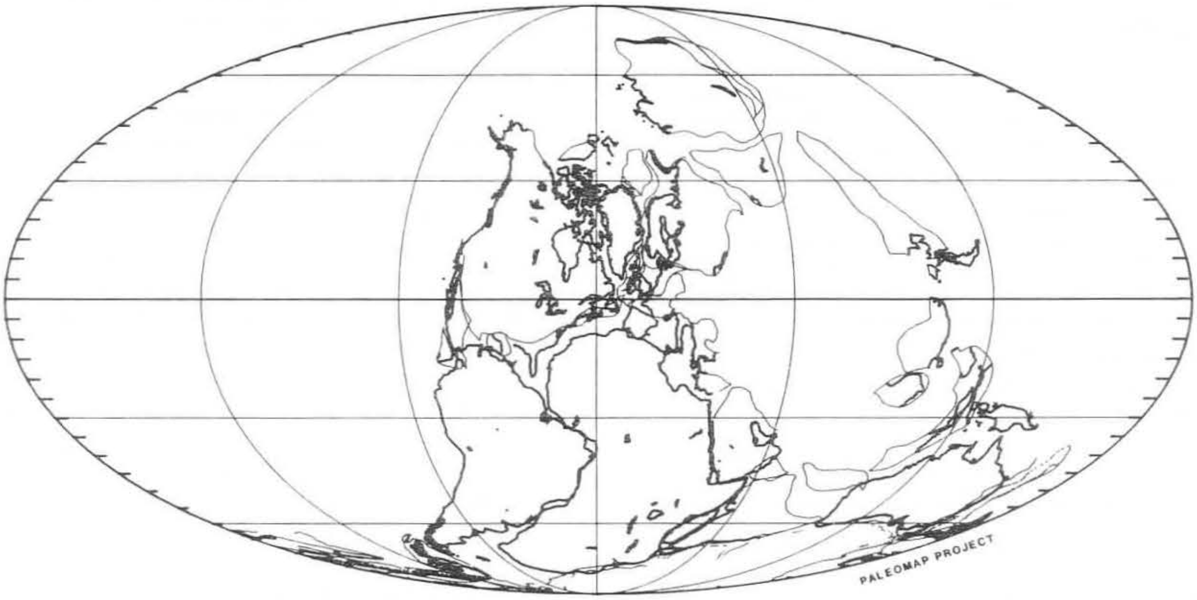


Plate Positions

Fig. 5.4. Generalized continental positions and orography in the Late Carboniferous. (Courtesy of C. R. Scotese and the PaleoMap Project, University of Texas, Arlington.)

Table 5.2 Upper Carboniferous Plants

Plant Group	Environmental Distribution	Habit	Reproductive Biology	Major Taxa
Lycopods	Peat and mineral substrate swamps	Mostly trees, some shrubs or herbs	Heterosporous, some with seedlike reproduction; many forms monocarpic, K-selected	Lepidodendron, Lepidophloios, Diaphorodendron, Sigillaria, Anabathra (Paralycopodites), Asolanus
Tree ferns	Flood basin habitats, including peat swamps in late Westphalian and Stephanian	Large and small trees	Homosporous; required some form of substrate exposure to reproduce; r-selected, weedy	Psaronius (Pecopteris); many species
Small ferns	Wide distribution; in most kinds of environments	Sprawling ground cover and vines	Mostly homosporous; extensive vegetative reproduction; span r/K spectrum	Botryopteris, Anachoropteris, Ankyropteris, Zygopteris, Psalixochlaena, Stauropteris
Pteridosperms	Better-drained parts of flood basins; in nutrient-rich parts of swamps	Large and small trees, ground cover vines	Seed plants; seeds ranging from small to very large; some possibly insect pollinated; many K-selected trees; some r-selected weedy forms	Medullosa and Sutcliffia (Common foliage types include Sphenopteris, Alethopteris, Neuropteris, Mariopteris, Odontopteris, Eusphenopteris), Callistophyton, Heterangium, Lyginopteris, other small forms
Sphenopsids	Wet parts of flood basins; high-energy aggradational environments	Trees (calamites) and shrubs (sphenophyllum)	Mostly homosporous; some heterosporous; most reproduction vegetative; more on K-selected end of spectrum	Arthropitys, Calamodendron, Calamites (Foliage types: Annularia, Asterophyllites), Sphenophyllum
Cordaites	Peat and mineral substrate swamps; undefined parts of wet floodbasins	Trees and shrubs, possibly mangroves	Seed plants; wind pollinated and dispersed; K-selected	Mesoxylon, Cordaixylon (Pennsylvanioxylon), Cordaites
Conifers	Well-drained areas, perhaps marginal-to-wet lowlands	Trees	Seed plants; wind pollinated and dispersed; K-selected	Walchia, Ernestiodendron, Hermitia

Although the same basic physical environments existed in the Stephanian as in the Westphalian, the distinction between peat-forming and other lowland vegetation types is blurred taxonomically (DiMichele et al. 1985). Peat swamps were dominated by ferns and pteridosperms (Phillips et al. 1985), as were surrounding flood-basin habitats (Pfefferkorn and Thomson 1982). A flora dominated by conifers and other distinct elements is clearly identifiable in more mesic, well-drained habitats by the Stephanian (Winston 1983; Mapes and Gastaldo 1986; Rothwell and Mapes 1988; Broutin et al. 1990; Mamay and Mapes in press). Its earlier existence in the Westphalian is suspected from allochthonous debris of conifers discovered in otherwise-typical lowland assemblages (Scott and Chaloner 1983; Lyons and Darrah 1989). The hints of a largely unsampled upland or inland flora suggest a large-scale bias in the tropical Late Carboniferous record (see chap. 2), possibly reflective of a low-relief landscape with a wide rainy belt (Parrish 1982; Ziegler 1990).

During the Westphalian, before major extinctions altered the basic flora that had evolved in the early Early Carboniferous, plant ecological dominance was distributed among lycopsids, ferns, sphenopsids, and seed plants (table 5.2). Within seed plants there were two major phylogenetic lineages, cordaites and pteridosperms, with environmentally distinct distributions. During the Stephanian, lycopsid trees ceased to be ecologically significant in all but a few habitats (Phillips et al. 1974; Phillips et al. 1985). Opportunistic ferns expanded to a dominant position in the wetter habitats, and seed plants, particularly cordaites and conifers, became important in a wider array of habitats. This proceeded as a stepwise loss of dominance by lower vascular (spore-producing) plant groups that were ecologically significant during the Early Carboniferous and Westphalian and continued through the Permian and into the Mesozoic (see chap. 6). Seed plants diversified and increased their ranges as other groups declined; this resulted ultimately in terrestrial domination by this one major clade of plants by the end of the Paleozoic. A similar pattern appears to have continued among lineages of seed plants.

Lycopsids

The lycopsid trees are better understood ecologically than any other group of Carboniferous plants. At least eight genera (DiMichele 1983, 1985; Wnuk 1989; Bateman and DiMichele 1991) and numerous species populated mainly peat and clastic swamp habitats. They ranged from dominants in physically stable habitats to colonizers of disturbed environments (DiMichele and Phillips 1985; DiMichele and DeMaris 1987; Gastaldo 1987). All lycopsids reflect a basic "pole-tree" architecture, with two variants. Some species had deciduous lateral branches on which cones were borne over an extended period of time (for reconstructions see Wnuk 1985, 1989; DiMichele and Phillips 1985). In many species individual trees spent much of their lives in a prereproductive phase, as an unbranched pole. In these species the development of a determinate crown signaled the beginning of reproduction, rendering the trees functionally monocarpic; the crown was the final phase of growth and can be envisioned as a reproductive adaptation rather than a light-capture structure. Many lycopsids produced massive, seed-like female reproduction units that appear to have been aquatically dispersed (Phillips 1979). Plant densities varied, but some lycopsid forests evidently had very high densities and high standing biomass per hectare (Gastaldo 1986b; DiMichele and DeMaris 1987; Wnuk and Pfefferkorn 1987). Some species may have formed small, high-density, monospecific patches within a more complex vegetation (DiMichele and Nelson 1989). The pole-tree forests were probably very open to light penetration, with random spacing between trees.

Lycopsid construction was relatively "cheap" compared to that of woody trees. The major support tissue was thick bark, which apparently was waterproof and decay resistant. The small amount of wood was very efficient at water conduction (Cichan 1986). There was no secondary phloem (Arnold 1960; Eggert and Kanemoto 1977); the lack of phloem presents a dilemma regarding the means by which the root systems of these trees received the sugars generated by photosynthesis. Anatomical aspects of the root system and their shallow burial suggest the possibility that leaflike rootlets borne on the stemlike stigmarian rhizomorphs were photosynthetic, and that roots and shoots independently generated their photosynthetic carbon (Phillips and DiMichele 1992). Leaves were sclerenchymatous and also lacked phloem or had little of it, suggesting very local use of photosynthate. Because the vegetative parts were composed of tough, lignified tissues containing few available nutrients, they offered little high-quality forage for insect of other arthropod herbivores, in spite of high total biomass. In contrast, large cones, both male and female, would have been likely targets for herbivory. Cones were produced in great numbers in monocarpic species, but only once in the life of a tree. Although it is not clear that whole stands reproduced synchronously, sedimentological factors associated with the preservation of in situ stumps (DiMichele and DeMaris 1987) suggest that some lycopsid stands may have been even aged.

Sigillaria was the only abundant lycopsid tree in Stephanian wetlands of Euramerica. Peat-forming wetlands of the early Stephanian were extremely variable in composition and included marshlands as well as forests (Phillips et al. 1974). When conditions favorable to the accumulation of thick, widespread peats returned, the remaining lycopsid trees did not regain their prior ecological prominence. Rather, tree fern and pteridosperm dominance of peat swamps ensued.

Pteridosperms

The taxonomic and structural diversities of pteridosperms were very high by the Late Carboniferous (Phillips 1981). Most medullosan pteridosperms were monoaxial trees (Pfefferkorn et al. 1984; Wnuk and Pfefferkorn 1984), 6 to

10 m in maximum height. Leaves were compound and could be several meters long (e.g., *Alethopteris;* Laveine 1986). These fronds were the dominant organs of the plant and had thick, leathery pinnules and robust construction. After death, frond remains may have folded back against the stem forming a "skirt" around the axis below the live crown: this is suggested by the recurved leaf bases found on many stems (Pfefferkorn et al. 1984). Such skirts may have provided important habitats for arthropods and small scansorial tetrapods.

Medullosans may have been poor quality food for herbivores. Stems had several bundles of vascular tissue, surrounded by secondary phloem (Delevoryas 1955; Stewart and Delevoryas 1956). However, these were buried in a dense ground tissue, including periderm, and stems retained leaf bases, further burying vascular tissue. In the frond axes vascular tissue was dispersed in small, isolated bundles (Ramanujam et al. 1974). Surrounding the vascular bundles and subepidermally in the stem and leaf axes were dense sclerenchymatous bundles. In addition, medullosan stems and leaves had abundant small canals filled with resinlike material (Lyons et al. 1982) that may have deterred insect predation. On the basis of the evidence, most arthropod damage to medullosan foliage (Scott and Taylor 1983) is not clearly due to herbivory, as opposed to detritivory. Lesnikowska (1989) notes no evidence of herbivory in an examination of hundreds of anatomically preserved coal-ball specimens, although Labandeira (1990) suggests possible leaf mining and folivory on the basis of damage to late Westphalian compression-impression medullosan leaves. In general, these plants appear to have been of tough construction and to have offered limited targets for either sucking or chewing on vegetative plant parts.

Reproductive organs, in contrast to vegetative parts, may have been major targets for predation. Although medullosan seeds were large, they were protected by complex seed coats, typically with hardened middle layers and fleshy outer layers (Taylor 1965). Seed-coat specializations may have protected the seeds against crushing or perhaps may have facilitated passage through the gut of herbivorous tetrapods or arthropods. In some cases, fleshy outer layers may have attracted animals. The great diversity in the size, shape, and anatomical structure of medullosan seeds suggests ecological specialization, possibly including close life-history associations with animals. Pollen organs (Millay and Taylor 1979; Stidd 1980) were very large in some species and contained large pollen grains, a potential energy source for animals that could tear through the tough outer layers of the reproductive structure (Kukalova-Peck 1983). Most medullosan pollen exceeded 200 μm in diameter, a size so large that animal—probably insect—pollination vectors are considered likely (Dilcher 1979).

A scrambling-to-viney habit was common among a wide diversity of small pteridosperms (Stidd and Phillips 1973; Rothwell 1981; Pigg et al. 1987). These plants generally produced small seeds and pollen organs, had sclerenchymatous plates or fibers in the stems and fronds, and had small compound leaves with relatively thin laminate foliage. Their vegetative parts and reproductive organs should have been accessible to low-browsing omnivorous or herbivorous tetrapods and arthropods. Most were very patchy in distribution, although some, such as *Callistophyton boysettii* of the late Westphalian (Phillips and DiMichele 1981; DiMichele and Phillips 1988) or *Lyginopteris* species of the early Westphalian (Phillips et al. 1985), were common and relatively abundant for such small plants. Fortuitous preservation of pollen drops and the morphology of some pollen grains indicate wind pollination in many of these taxa (Rothwell 1972, 1977).

Throughout the Late Carboniferous, pteridosperms were dominant elements on clastic soils of floodplain habitats (Peppers and Pfefferkorn 1970; Scott 1977, 1978, 1979; Pfefferkorn and Thomson 1982). Their numbers increased in peat swamps during the Westphalian, although only a few genera from clastic-compression floras were able to grow in peat-forming environments. No species were unique to peat swamps (DiMichele et al. 1985).

Pteridosperms produced relatively large amounts of litter. In some trees much of the litter may have remained in the crowns as fronds died and decayed while still attached to stems; in others, such as many neuropterid species, pinnules abscised and the recurved rachises may have added support to the slender stems (Pfefferkorn et al. 1984).

Ferns

Ferns were important in most lowland environments during the Westphalian and Stephanian. They can be divided into two major groups: herbaceous ground cover, including vines; and trees or subtrees. Epiphytic habit has been suggested for some ferns, although the evidence is equivocal (Rothwell 1989). Small ferns were present throughout the Westphalian (Phillips 1979) at a low biomass (1% to 5%) but in considerable taxonomic and structural diversity. Tree ferns, some of which were of low stature, specifically the marattialean *Psaronius*, were present in low but increasing numbers up to the late Westphalian, when tree-fern abundances rose rapidly throughout the Euramerican lowlands (Phillips et al. 1974; Pfefferkorn and Thomson 1982; Phillips and Peppers 1984). Marattiales appeared first in peat-forming environments during the middle Westphalian, perhaps in the nutrient-poor central areas of raised peat bodies (Eble 1990). It is not clear that these populations were ancestral to later peat-swamp or floodplain marattialean ferns. During the Stephanian, tree ferns were the dominant trees in most peat swamps (Phillips and Peppers 1984) and in many other habitats (Pfefferkorn and Thomson 1982).

Small ferns were among the most important ground-cover elements during the Late Carboniferous (e.g., *Psalixochlaena, Botryopteris, Anachoropteris, Ankyropteris, Zygopteris, Stauropteris*). Most were of sprawling habit, many perhaps were facultative climbers similar to poison ivy (J. Mickle, pers. comm. to DiMichele 1987), and some were true vines (Millay and Taylor 1980, Trivett and Rothwell 1988). Small but abundant fronds, thin laminate foliage, and little or no sclerenchymatous or woody tissue characterize these plants as a group (Phillips 1974). Reproductive organs varied in complexity, but some, such as those of *Zygopteris* and some *Botryopteris* species, were produced in large, armored aggregations (Murdy and Andrews 1957; Phillips and Andrews 1968; Galtier 1971) that would have been accessible to foraging animals. Most reproductive organs were foliar borne, which may have discouraged predation, because the nutrient-rich tissues were dispersed and would have caused animals to ingest less-digestible vegetative tissue along with energy-rich sporangia.

Marattialean ferns were uncommon and of low taxonomic diversity throughout much of the early Westphalian (Corsin 1948; Millay 1979; Pfefferkorn and Thomson 1982; Gastaldo 1984; Phillips et al. 1985). Beginning in the middle Westphalian and accelerating during the late Westphalian, this group of plants diversified and became a dominant element of many kinds of vegetation. Even more so than lycopsids, marattialeans of tree habit were "cheaply" constructed. They attained aborescence by mantling a relatively fleshy stem of small diameter in a thick cover of supporting, adventitious roots (Ehret and Phillips 1977). The roots were mostly air spaces and provided strength in aggregate. Fronds several meters long were borne in an umbrella-like crown. *Psaronius* foliage was thin but often bore reproductive organs in high density on the undersides of pinnules (Millay 1979). Many species contained sclerenchyma bundles and sheaths in leaves and stems and, less commonly, very abundant mucilage ducts or cavities throughout stem and leaves (Morgan 1959; Mickle 1984). "Cheap" construction, high dispersal abilities, and tolerance of all but deeply flooded physical environments led to the ecological expansion of this plant group.

Psaronius plants probably were major targets for herbivores, particularly insects. At present there is little supporting evidence for this hypothesis except for a report on wound repair associated with tissue damage and fecal pellets in Stephanian-age *Psaronius* fronds (Lesnikowska 1990). Lesnikowska (1989) also has found a major size difference between Westphalian and Stephanian *Psaronius* species in peat swamps; whereas Westphalian forms generally were small subtrees, larger, heavily root-mantled stems appear in the later Westphalian and become characteristic in the Stephanian. Such increased size would have kept all but climbing and flying animals from the fertile fronds of *Psaronius*.

Sphenopsids

There were two major groups of sphenopsids during the Carboniferous, both clonal. The sphenophylls were ground-cover plants and the calamites were arborescent forms. *Sphenophyllum* encompassed many species and occurred in almost all lowland habitats. In general the plants were sprawling, with small woody stems and delicate heterophyllous leaves borne in whorls. Batenburg (1982) differentiates peat-swamp species from those of other environments. In floodplain and streamside settings, many *Sphenophyllum* species apparently formed dense thickets of highly branched stems linked by barbs or hooks on the leaves. These thickets may have been almost impenetrable to large animals and were possibly favored by smaller, relatively defenseless forms. Densities of *Sphenophyllum* in shales frequently are high, with stems crossing bedding planes vertically, suggesting partial burial in place and an ability to survive such burial. Although abundances of *Sphenophyllum* were patchy in peat swamps, local densities could be high; there is no evidence of interlocking of the stems and leaves in such assemblages. Cones were of small to moderate size, and sexual reproduction may have been secondary to clonal growth as a means of local spread in such environments.

Calamites were the only trees of the Late Carboniferous that were clonal (Tiffney and Niklas 1985). They were variable in size and form (Hirmer 1927) but could be quite large trees. The largest woody stems, almost 0.5 m in diameter, have been found in Stephanian-age coal-ball deposits (Galtier and Phillips 1985). Westphalian calamites appear to have been of smaller girth and presumably were shorter than the largest Stephanian forms. They were most abundant in streamside habitats, such as channel bars, at lake margins, and in other near-water settings (Oshurkova 1974; Brzyski et al. 1976; Scott 1978). In these environments, vegetative clonal growth was probably significantly more important than sexual reproduction. Although they were occasionally the dominant element of physically disturbed wetland habitats, calamites were minor components of the vegetation for the most part. Woody stems, thin leaves, and relatively low reproductive allocation suggest that they were not significant targets for herbivores.

Cordaites and Conifers

Cordaites were a diverse group of woody plants related closely to the modern conifers (Mapes 1987). They ranged from large forest-forming trees, encountered almost exclusively in deposits associated with well-drained, clastic-soil habitats, to small, thicket-forming shrubs that were possibly mangrovelike within peat-swamp environments (Raymond and Phillips 1983; Rothwell and Warner 1984; Costanza 1985; Trivett and Rothwell 1985; Raymond 1988). The biology and ecology of peat-swamp cordaites is much better known than that of nonswamp taxa.

Cordaites had dense wood. Leaves were typically strap shaped and in most species were coriaceous, with thick cuticle and abundant sclerenchyma. Winged seeds with large nutrient reserves often were produced in abundance in exposed positions on small conelike shoots. In general these seeds, of which several different types are known, had a very sclerenchymatous seed coat that may have deterred predation by animals (for discussion of cordaite seed structure, see Roth 1955; Leisman 1961; Taylor and Stewart 1964). In most instances papery wings suggest wind dispersal, although in *Cardiocarpus magnicellularis* a fleshy outer seed coat (Baxter and Roth 1954) may have attracted certain animals. Both attractant and protective aspects of these seeds could have functioned after, as well as before, dispersal.

Cordaites were abundant in peat swamps during the middle and late Westphalian but were minor elements of Stephanian swamps. In lowland areas peripheral to peat formation (traditionally "uplands" or "extrabasinal lowlands"; Havlena 1970; Pfefferkorn 1980), they appear to have been important trees from the earliest Late Carboniferous (Leary 1981). Occurrences of cordaitean trees continued into the Stephanian and Early Permian (Winston 1983; Lyons and Darrah 1989) on better-drained, clastic soils.

Conifers occurred first in the middle Westphalian (Scott and Chaloner 1983; Lyons and Darrah 1989) as fragmentary allochthonous material and as microfossils in areas adjacent to contemporaneous uplands. They are encountered rarely in Westphalian rocks. Several occurrences in the late Westphalian are discussed by Lyons and Darrah (1989), again largely from areas proximal to contemporaneous "uplands," or areas of erosion. The oldest well-preserved conifers in the Appalachian basin appear at or near the Westphalian-Stephanian boundary (McComas 1988). Conifers are more commonly encountered in Stephanian assemblages (Cridland and Morris 1963; Winston 1983; Mapes and Gastaldo 1986; Rothwell and Mapes 1988; Mapes and Rothwell 1988), mostly in habitats peripheral to peat formation and, rarely, from strata associated with coals (Canright and Blazey 1974; McComas 1988).

The primitive conifers *Walchia* and *Ernestiodendron* (*Hermitia* and *Culmitzchia* if not differentiable to one of the other genera; Visscher et al. 1986) were similar to many modern conifers vegetatively, with needlelike leaves, wood, tree habit, and moderate-to-large size (Florin 1951; Visscher et al. 1986). The cones were not as compact or as well protected against predation as those of modern conifers (Mapes 1987), but they may not have been accessible to large arthropods or low-browsing tetrapods. These trees apparently tolerated drier, better-drained conditions, as suggested by both their structure and the sedimentary contexts in which they are most often preserved (Winston 1983; Mapes and Gastaldo 1986; Rothwell and Mapes 1988; Lyons and Darrah 1989; but see McComas 1988). Woody stems, evergreen leaves, seed dormancy (Mapes et al. 1989), and co-occurrence with large cordaites in a seed-plant-dominated vegetation suggest growth in stable habitats with xeric conditions at least part of the year. At some sites, such as the earliest conifer from England or the Stephanian-age deposits at Garnett and Hamilton Quarry, Kansas, conifer remains are often preserved as fusain, suggesting forest fires and periodically fire-prone or water-stressed habitats (Scott and Chaloner 1983; Rothwell and Mapes 1988). These conifers probably would have been relatively low-quality forage; as with cordaites, early herbivores may have been interested only in their seeds or pollen.

6.2 Invertebrates

The record of Westphalian and Stephanian terrestrial invertebrates indicates a broad ecological spectrum, approximating that of post-Paleozoic to modern faunas, though diversity is not comparable. Nearly all information comes from lowland, equatorial areas of peat accumulation (Wootten 1981; Durden 1984a). The record includes the first appearance of terrestrial molluscs (Solem and Yochelson 1979). Most of the information on arthropods comes from collecting sites that have exceptional preservation, such as Mazon Creek (late Westphalian, Illinois), or Commentry and Montceau-les-Mines (Stephanian, France), which present opportunities to study diversity and anatomy. Supplementing these deposits are other, less prolific assemblages, such as those in roof shales above coals (Jarzembowski 1987) or from coals (Bartram et al. 1987), which provide an important indication of distribution. The most common arthropods are myriapods, arachnids, and insects, particularly blattoids. The greatest diversity is recorded at Mazon Creek, the most intensively studied assemblage. Ecological inferences are based in large part on functional analyses of mouthparts in living relatives and on the nature of damage to plants.

Detritivores

A large proportion of primary plant productivity in the Westphalian and Stephanian continued to reach animal food webs through arthropod detritivores. A great variety of detritivores are known or suspected. Among the most abundant terrestrial arthropods were millipeds and arthropleurids. Millipeds appear to have had the same ecological role as today, namely, as detritus feeders and soil formers in forested regions. The Late Carboniferous record included cylindrical forms, which burrowed or pushed through soft substrates, and flat "litter splitters" (Hoffman 1969; Rolfe 1985a). Spiny millipeds, both flat and cylindrical, were more common in the Late Carboniferous than today (Hannibal and Feldman 1981), and some probably were too large to hide in litter. Evidence of damage to spines (Rolfe 1985a) suggests predation by amphibians and reptiles, some of which swallowed prey whole. Rolfe (1985a) and others have suggested further that some Carboniferous myriapods may have had the protection of repugnatorial glands, similar to those in extant forms.

Arthropleurids were of enormous size by the Late Carboniferous, perhaps greater than 2 m in length (Rolfe and Ingham 1967; Rolfe 1980; Hahn et al. 1986). Evidence from gut contents indicates that their diet included wood as well as higher nutrient materials. The large size of archipolypod millipeds and arthropleurids and the presence of long tergal spines in the former suggest that these animals filled a niche not yet shared with tetrapods. Whether the demise of archipolypods and giant arthropleurids was due to increasingly effective predators, competition from predators, extensive environmental disruption, or some combination of these is unclear. Though not giant, large myriapods live in tropical to temperate regions today.

Among chelicerates, mites may have been detritivores during the Late Carboniferous, but coprolites provide the only evidence of these animals (Scott and Taylor 1983). Mites may not have radiated by this time into the diversity of ecological roles they have today, and most mites probably fed on fungi and the wood these fungi invaded.

Hexapods included several important detritivorous groups. Among insects, blattoids ("roaches") were the most widespread and abundant arthropods of the Carboniferous (Durden 1969, 1984a, 1984b, 1988; Wootten 1981; Scott and Taylor 1983). The extinct order Protelytroptera, ancestors of modern earwigs, were beetle-like. Collembolans also are inferred to have been important detritivores, despite a lack of fossils in the Carboniferous, because of occurrences in both Devonian and Permian strata (Riek 1976; Greenslade and Whalley 1986).

Herbivores

Insect herbivory appears to have been well developed by the Late Carboniferous. Chewed leaves, bored seeds, and pollen in coprolites and guts (Scott and Taylor 1983) all suggest herbivory, although such damage could be post mortem. Inferences drawn from insect functional morphology (e.g., Labandeira 1990; Labandeira and Beall 1990), however, reinforce the herbivory interpretation, as does evidence of plant-tissue repair and characteristic feeding patterns, such as leaf mining (Labandeira 1990). The rise of insect herbivory may have been related indirectly to the evolution of wings in the Early Carboniferous. With flying abilities, insects no longer were limited to a cryptic habit (Durden 1984a) and could exploit new resources. Such herbivory would have enhanced the entry of plant primary productivity into animal food webs and greatly strengthened links between animal and plant communities.

The paleopteran orders Megasecoptera and Paleodictyoptera included a variety of forms, with wingspans ranging from 9 mm to 43 cm. Wings of the adult insects were permanently outstretched horizontally. This configuration affects abilities to perch under windy conditions, makes walking difficult, constrains flying to areas of open vegetation, and limits hiding places (Carpenter 1971). Complex color patterns on the wings of Paleodictyoptera may have served as disruptive concealment, apostematic warnings, or perhaps even communication in mating or mate competition. The animals may have preferred open vegetation beneath moderately dense canopies, which could be found in pteridosperm or tree-fern-dominated areas. Both nymphs and adults of many species were armored or spiny, suggesting antipredator adaptations.

Mouthparts of megasecopterans and paleodictyopterans were modified for piercing and sucking; some paleodictyopteran species had a pronounced cibarial pump. In *Monsteropterum moravicum*, the beak was 20 cm long and contained two mandibular and two maxillary stylets and one hypopharyngeal stylet; all rested in a Z-shaped labial trough (Kukalova-Peck 1972, 1985). Such insects may have torn apart fructifications with claws and imbibed the spore or pollen contents (Kukalova-Peck 1983); spores have been found filling the guts of larger specimens of several species. Bored holes in seeds and megaspores (Sharov 1973; Scott and Taylor 1983) suggest predation by sucking insects. Sap feeding from vegetative tissues, specifically phloem, also may have occurred (Scott and Taylor 1983), although Kukalova-Peck (pers. comm. to Shear 1987) argues that sap feeding requires mouthparts that are not found in these insects and that only the small species fed on sap, probably from ovules rather than stem or leaf phloem. Certainly most Late Carboniferous lowland plants were not optimal targets for vegetative herbivory (thick bark, little or highly dispersed phloem) but did present easily accessible megaspores, ovules, and microspores or pollen. Nymphs of these orders also were winged, terrestrial forms and apparently were herbivorous, feeding mostly on fructifications (Kukalova-Peck 1978; Shear and Kukalova-Peck 1990).

Among the Neoptera, herbivores included the Protorthoptera (Burnham 1983) and several other related groups in the Hemipteroidea (Rasnitsyn 1980), and the Orthoptera (Sharov 1968). Hemipteroidea in general were diverse and abundant in the Carboniferous, with a variety of mouthparts, from those for chewing or sucking with a domed postclypeus to those with triangular or elongated stylets. The Protorthoptera had chewing mouthparts, although some had raptorial, mantislike front legs (Carpenter 1971). Among Orthoptera, most of the modern ecomorphs were present in the Permo-Carboniferous. As in modern forms, hind legs were adapted for jumping, and biting mouthparts were present, suggesting herbivory.

Predators

Predatory chelicerates and insects were common and diverse in Westphalian and Stephanian communities. Some of the forms were probably in resource competition with tetrapods, and the Late Carboniferous may have been a transitional time in the relationship between arthropod and tetrapod predators. Among chelicerates, scorpions and arachnids were the major terrestrial predators. Scorpion cuticle has been recovered in large quantities from macerations of British coals (Bartram et al. 1987), indicating the presence of scorpions in peat-forming habitats, as well as in better-drained settings (Kjellesvig-Waering 1986). Predatory arachnids included large, heavily armored trigonotarbids (aphanototarbids) with reduced eyes, and the closely related anthracomartids, which were eyeless; both lacked web-building or poison glands. These groups are rare but diverse at Mazon Creek (Richardson and Johnson 1971). All Late Carboniferous spiders belong to the suborder Mesothelae. They were small and very much like their modern descendants, except *Megaranea* (Hünicken 1980), which had a leg span of more than 40 cm. Present-day relatives of these spiders build silk-lined burrows. Evidence for extensive use of silk in aerial webs in the Upper Carboniferous is scant and ambiguous. The earliest clear indication of web-building capabilities is from the Triassic in fossils that appear modern morphologically. Other arachnid groups of the Late Carboniferous were the phalangiotarbids, a group of sit-and-wait, spiderlike predators (Beall, pers. comm. to Shear 1987), the Uropygi and Amblypygi, also sit-and-wait predators, and the Opiliones and Solpugida, which were voracious, active hunters. The Ricinulei were larger and more diverse predators in litter during the Carboniferous than today (Selden 1986).

Predatory insects of note are the Protodonata (dragonflies) and Ephemerata (mayflies). Protodonata are common as fossils because they frequented lake and pond margins and had aquatic larvae (Kukalova-Peck, pers. comm. to Shear 1987). The protodonata often reached large sizes, with wing spans up to 63 cm reported for Stephanian forms (Carpenter 1960). However, wingspans of as little as 30 mm have been reported (Wootten 1981), which is small even by modern standards. The legs of the larger animals were proportionately more robust than those of extant dragonflies, suggesting that they caught large insects in flight. Ephemerata are rare in the Late Carboniferous, but giant forms with wingspans up to 42 cm are known from Germany and Illinois (Kukalova-Peck 1983). Adults differed from modern mayflies in having functional biting mouthparts. Their aquatic larvae may have preyed upon small aquatic vertebrates.

In summary, the spectrum of Paleozoic predatory arthropods was quite different from that of today. They tended to be much larger, and species diversity may have been lower. Most of the arachnids were cursorial or sit-and-wait predators. There probably were no web-building spiders. Predaceous arthropods may have preyed upon herbivorous and detritivorous arthropods, which had increased greatly in abundance and diversity over earlier times, or on small tetrapods. Herbivorous forms were more numerous and more diverse than predators by the Late Carboniferous, a reversal of previous conditions.

6.3 Vertebrates

Late Carboniferous terrestrial amphibians and amniotes are known mainly from eleven extensively collected deposits that are dominated by aquatic-to-amphibious taxa and from five localities that are distinguishable as terrestrial assemblages. The records are from southern Euramerica. Nearly all Westphalian-age examples occur in coal-bearing, fluviodeltaic sequences and represent autochthonous samples of tropical wetland faunas (Gersib and McCabe 1981; Rust et al. 1984; Hook and Ferm 1988; Hook and Baird 1988). In contrast, a great range of paleoenvironmental circumstances is presented by Stephanian tetrapod-bearing deposits; these include, but are not limited to, sapropelic fillings of small lakes and clastic fillings of small-to-large lakes (Boy 1977), carbonaceous and calcareous channel fills within well-drained coastal settings (Reisz et al. 1982; French et al. 1988), and braided stream deposits within semiarid alluvial plains (Berman et al. 1987a; Eberth 1987). Although a few Stephanian examples are taphonomically comparable to those of the Westphalian, no Westphalian deposit has the better-drained edaphic aspects of certain Stephanian localities.

The exceedingly narrow paleoenvironmental scope of Westphalian tetrapod occurrences has confounded evolutionary and ecological interpretations. Some of the more terrestrial elements of the fish-dominated assemblages, for example, have been regarded as "erratics" from an otherwise unsampled "uplands" biota (A. R. Milner 1980a; Boyd 1984; Olson 1985a), a notion that appears to be supported by upright tree stumps that contain terrestrial forms (Carroll et al. 1972). Sedimentological and petrographic data (Hook and Hower 1988), however, reveal that such distinctions are artificial and that aquatic, amphibious, and terrestrial animals coexisted at a landscape scale within a mosaic of lowland habitats. Thus, like most of the autochthonous plant deposits, the present Westphalian tetrapod sample is of use in discussing only one type of Late Carboniferous ecosystem.

A small number of Stephanian vertebrate localities also offer plant assemblages that suggest well-drained substrates or dry climatic conditions. Taxonomically, however, none of the Stephanian assemblages appears to be the lineal descendant of faunas from the Westphalian wetlands; rather the assemblages are composed of amphibian and amniote groups that persist well into the Early Permian, a pattern paralleled to a large extent by the associated plants (Mapes and Gastaldo 1986).

In both ecological and morphological terms, most Paleozoic tetrapods cannot be portrayed fairly by simple analogy to modern forms. Because many of the major groups of Late Carboniferous land-dwelling amphibians and reptiles are extinct, only ecomorphic generalizations, based mainly on postcranial morphologies and to a lesser extent on sensory adaptations, are possible. Interpretation of several amphibian groups is hindered further by the likelihood that individual taxa had strong life-history ties to aquatic environments and may have become active in nonaquatic setting only as adults.

Anthracosaurs

Two types of anthracosaur amphibians, embolomeres and gephyrostegids, are known from Westphalian coal deposits. Several embolomere genera, in particular *Anthracosaurus* (Panchen 1977, 1981) and similar North American taxa, have been interpreted as possible terrestrial forms. Although this is difficult to assess without more complete representation of postcranial skeletons, their massive dentitions and deep skulls indicate a predatory habit. On the other hand, gephyrostegids were short-trunked, generally lightly built tetrapods that averaged approximately 0.4 m in total length (Carroll 1970) and probably were insectivorous. They are known first from a nearly complete skeleton from the Namurian of Germany (Boy and Bandel 1973). The largest gephyrostegid is the enigmatic reptiliomorph *Solenodonsaurus*, a more robust form from the late Westphalian (Carroll 1970; Panchen 1972).

Fragmentary remains of archeriid embolomeres occur in both Westphalian and Stephanian rocks of North America. On the basis of their similarity to the well-known genus *Archeria* from the Lower Permian (Romer 1957; Clack and Holmes 1988; Holmes 1989), these Upper Carboniferous records probably represent an intermediate-sized gavial-like form that was primarily aquatic.

Nectrideans

Despite an abundance of nectrideans in Upper Carboniferous vertebrate deposits, only *Scincosaurus* appears to have been suited for terrestrial existence. This genus is known from both Westphalian and Stephanian coal-bearing facies. A small, short-bodied form with a long, relatively inflexible tail, *Scincosaurus* exhibited robust girdles and limbs indicative of a nonaquatic habit. A disproportionately small skull and small pedicellate teeth suggest a diet of soft-bodied prey (A. C. Milner 1980).

Microsaurs

Microsaurs were small, predominantly terrestrial amphibians. Although microsaurs are present at several Westphalian localities, the Stephanian record of land-dwelling taxa is poor. *Tuditanus*, a well-known late Westphalian genus (Carroll and Baird 1968), was a small (approximately 15 cm total length), superficially salamander-like form that probably fed on insects and other small arthropods; other tuditanomorphs reached a length of approximately 30 cm (*Asaphestera*, Carroll and Gaskill 1978; *Trihecaton*, Vaughn 1972). Other Late Carboniferous microsaurs, such as *Elfridia* (Thayer 1985), *Leiocephalikon*, and *Sparodus* (Carroll 1966), possessed crushing dentitions of large, blunt, conical teeth set in massive jaws and in some cases sets of large accessory teeth. Such species probably had an omnivorous diet of hard-shelled invertebrates and possibly nutrient-rich, hard-covered seeds.

Temnospondyls

The greatest variety of terrestrial amphibians during the Late Carboniferous is found in the Temnospondyli. As a group, they ranged from small to intermediate-sized insectivores and carnivores that were highly terrestrial, to large carnivores that probably favored marginal aquatic settings and a main diet of freshwater fish, sharks, and amphibians. *Dendrerpeton*, known from the early Westphalian of Ireland and Nova Scotia, represents a generalized design with a boxlike skull and well-ossified, modestly scaled postcranial skeleton; dentition consisted of marginal tooth rows of many simple conical teeth accompanied by palatal tusk pairs and finely denticulated palatal surfaces (Carroll 1967a; A. R. Milner 1980b). A primitive impedance-matching system for perception of air-borne vibrations may have been present (Clack 1983; Godfrey et al. 1987). Although no complete skeletons have been described, ample specimens indicate a small terrestrial form that probably fed on invertebrates.

By the late Westphalian, the major amphibious-to-terrestrial temnospondyl groups were differentiated. Westphalian edopoids are known best from *Cochleosaurus*, a long-skulled, crocodile-like form (Rieppel 1980; A. R. Milner 1980a). The preponderance of small to intermediate-sized specimens in a large sample of over 50 individuals from Nýřany, Czechoslovakia, suggests increased terrestriality with growth. Large individuals exceeded 1.5 m in length and appear to have been sit-and-wait predators. More primitive edopoid genera are known from the early Westphalian, and others are present in late Westphalian assemblages (Milner 1987).

Amphibamus, a salamander-like form of late Westphalian age, is the oldest representative of the Dissorophoidea, a group of terrestrial Permo-Carboniferous temnospondyls that is characterized by, among other features, a froglike stapes and, presumably, a tympanic ear (Bolt and Lombard 1985). Growth stages of *Amphibamus* range from larval forms with external gills to fully terrestrial adults with estimated body lengths up to 25 cm (Bolt 1979; Milner 1982; Hook and Baird 1984). A similar genus is recorded in the Stephanian (Daly 1988, in press). The trematopids are a second group of Late Carboniferous dissorophoids that have a conventional body design. They are interpreted as land-dwelling forms on the basis of marginal dentitions, which consisted of small but acuminate, moderately recurved teeth, and general skull morphologies. The posterior part of the elongated narial opening of trematopids has been interpreted as the site of a salt gland comparable to that in some modern lizards (Bolt 1974b). Trematopids are known from the Westphalian (*Mordex;* Milner 1986) and the Stephanian; postcranial remains from the Stephanian of Kansas and New Mexico suggest body lengths of up to 50 cm (Milner 1985; Berman et al. 1987a).

Two groups of aberrant dissorophoids that are regarded traditionally as Permian forms are recorded in middle to late Stephanian deposits. Genera from Ohio and the southwest United States had bizzare pelycosaur-like "sails" composed of greatly extended and somewhat expanded neural spines (*Astreptorhachis*, Vaughn 1971; *Platyhystrix*, Berman et al. 1981). They reached a meter or more in body length and appear to have been fully terrestrial carnivores. The second group, the so-called armored dissorophoids, were somewhat smaller and are discussed in §7.3, Temnospondyls.

Remains of eryopoids are recorded in early Stephanian deposits. The Appalachian species of *Eryops* exceeded a meter (Vaughn 1958; Murphy 1971) in length and was probably an amphibious-to-terrestrial carnivore as an adult. Actinodontids and other eryopoids from the Permo-Carboniferous of Europe (Boy 1988, 1990) generally were smaller and even less terrestrial.

Aïstopods

Two distinct aïstopod amphibian families occurred in the Late Carboniferous. Ophiderpetontids, which reached a length of nearly 2 m, are regarded as the more aquatic group (A. R. Milner 1980a), whereas the generally smaller and less heavily scaled phlegethontids show several specializations that may represent terrestrial adaptations (McGinnis 1967). For example, a radically modified skull may have allowed certain phlegethontid genera to ingest oversized prey in a manner similar to that of some modern-day snakes (Lund 1978).

Cotylosaurs

Cotylosaurs (*sensu* Heaton 1980) have long attracted attention because they offer a blend of amphibian and reptilian characters in what has been regarded classically as *the* primitive terrestrial morphotype. Limnoscelids are represented by fragmentary remains from three North America localities that range from late Westphalian to early Stephanian age (Carroll 1967b, 1984; Berman and Sumida 1990). Recognition of these materials, however, relies on a virtually complete skeleton of *Limnoscelis* from the upper Stephanian or possibly lowermost Permian of New Mexico (Romer 1946; Fracasso 1980, 1987). Despite the size of this specimen (nearly 2 m in total length), a poorly ossified postcranial skeleton implies an amphibious, perhaps crocodile-like habit.

Diadectid cotylosaurs, the earliest possible herbivorous tetrapods known at present, first appear in the early Stephanian (Carroll 1984) and range from the southwestern United States through the Ohio Valley to central Europe. The larger Stephanian diadectids equal the dimensions of small *Diadectes* specimens from the Lower Permian (Vaughn 1969, 1972) and are characterized similarly by chisel-shaped "incisors" and transversely expanded cheek teeth that show wear facets; however, both the degree of expansion and amount of wear on the teeth of Stephanian forms are significantly less than those exhibited by Permian diadectids. Short, broad limbs indicate limited locomotor abilities and suggest a diet of only slow-moving, if not stationary, low-to-the-ground objects. Shelled invertebrates, seeds, and pollen-bearing organs that required crushing are plausible food items; living plant materials, such as roots and low-to-the-ground shoots or foliage, cannot be excluded, but lack of extreme tooth wear such as that seen in later much larger diadectids suggests that Stephanian representatives were omnivorous. The increased body size and greater dental specialization of Permian diadectids suggest a change in feeding habits during the Permo-Carboniferous.

Amniotes

The Late Carboniferous vertebrate record is distinguished by the first representation of a diverse amniote stock. Two major groups, the captorhinomorphs and the synapsids, appear in Westphalian coal-bearing facies, and a third clade, the diapsids, is known mainly from a wealth of specimens from a single Stephanian locality. Whereas Carboniferous captorhinomorphs and synapsids appear as generalized forms transitional to the far greater array of amniote ecomorphotypes seen in the Early Permian, diapsids show comparatively little change through this time period. The unheralded appearance of well-differentiated amniote clades in the late Westphalian, along with insights provided by the recent East Kirkton discovery (Smithson 1989), underscore the inadequacies of our present sample of early tetrapod faunas.

Protorothyridid captorhinomorphs are well known as small (average body length of approximately 20 cm), lizardlike forms that appear first in Westphalian coal-bearing facies (Carroll and Baird 1972). The closely spaced, bluntly pointed, conical teeth of the marginal series indicate that the protorothyridid captorhinomorphs were insectivorous, and elongation of the limbs suggests an active existence that may have included tree climbing (Reisz and Baird 1983). Protorothyridid remains are very poorly represented in the Stephanian record, but trackways corresponding to their pedal morphologies and body proportions are known.

The pelycosaur *Archaeothyris* is the only Westphalian-age synapsid represented by reasonably good fossil material (Reisz 1972, 1975). Over 50 cm long, this form exhibits a high skull with sharp, slightly recurved and compressed teeth that bear modest serrations. These attributes, along with those of its poorly known postcranial skeleton, indicate that *Archaeothyris* was a terrestrial predator.

A rich diversity of pelycosaurs is recorded at Garnett, Kansas, in a Stephanian-aged channel fill that occurs within a carbonate-dominated coastal plain setting (Reisz et al. 1982); as noted above, the Garnett plant assemblage is characterized by taxa that suggest well-drained substrates and perhaps seasonally dry climate. The Garnett edaphosaurid, *Ianthasaurus*, is particularly noteworthy because of its relatively small size (50 cm estimated length) and insectivorous dentition (Reisz and Berman 1986; Modesto and Reisz 1990); later edaphosaurids were much larger, with more specialized dentitions, bulky trunks, and small heads.

The sphenacodontid *Haptodus* occurs first at Garnett and is the earliest representative of a very successful group of dominant terrestrial predators. Also known from excellent European materials, the postcranial skeleton represents an agile but powerful form, and the marginal dentition features well-differentiated caniniform teeth and modifications for slicing rapidly through prey (Currie 1977, 1979). Another sphenacodontid from Garnett has a more massive, bulbous dentition that suggests a somewhat different diet (Reisz 1990). A much larger (over 3 m in estimated length) sphenacodontid occurs in Stephanian coal deposits of Czechoslovakia, though it is represented only by incomplete material (Romer 1945; Zajíc and Stamberg 1985).

Upper Stephanian to possibly lowest Permian deposits in New Mexico, representing better-drained or drier habitats, have furnished fragmentary remains of large varanopseid pelycosaurs that exceeded one meter in length (Romer and Price 1940; Eberth and Brinkman 1983). By comparison with slightly younger varanopseids from the same region, these early synapsids were dominant predators, although more lightly built than contemporaneous sphenacodontines.

A lizardlike habitus typifies the Stephanian diapsid *Petrolacosaurus*, which occurs in abundance at Garnett (Reisz 1981). In comparison with protorothyridids, the longer limbs, neck, and tail impart a more gracile appearance to this larger but also insectivorous form.

Characteristics of Terrestrial Vertebrate Faunas in the Late Carboniferous

Table 5.3 summarizes the size ranges and feeding habits inferred for terrestrial tetrapods of the Westphalian and Stephanian. Although these gross ecological groupings suggest a dichotomy between small insectivores and medium-sized carnivores, there was almost certainly overlap; insectivores preyed upon a variety of small animals, including other tetrapods, and predators of intermediate size probably also consumed a mixed diet of smaller tetrapods and some arthropods. Large predators are represented by several anthracosaurs and temnospondyls, which may have been more amphibious and adapted to passive sit-and-wait strategies, and by intermediate- to large-sized sphenacodontid pelycosaurs, which were undoubtedly more active and probably attacked amphibious-to-terrestrial tetrapods of any size with success.

Increased size in diadectids through the Permo-Carboniferous interval may have conferred certain physiological advantages, such as an ability to utilize high-fiber plant tissues, but also may have been a response to predator pressures. Given the abundance of vertebrate insectivores and predatory insects, a similar interpretation may account for the appearance of very large representatives of several arthropod groups in the Upper Carboniferous.

In all Westphalian assemblages, associated with peat formation and presumably very wet conditions, terrestrial carnivores were outnumbered by insectivores. This relationship is difficult to evaluate in the Stephanian because assemblages are few and samples are small, but it is clearly reversed in a majority of Early Permian assemblages. There is no unequivocal evidence of terrestrial herbivores in the Upper Carboniferous, but some forms, the om-

Table 5.3 Upper Carboniferous Terrestrial Amphibians and Reptiles

	Small	Intermediate	Large
Carnivores	Phlegethontid aïstopods	Ophiacodontid pelycosaurs Sphenacodontid pelycosaurs Varanopseid pelycosaurs Solenodonsaurid anthracosaurs "Platyhystrixid" and trematopid temnospondyls	Sphenacodontid pelycosaurs Anthracosaurid anthracosaurs? Edopoid temnospondyls Eryopoid temnospondyls Limnoscelid cotylosaurs?
Insectivores	Protorothyridid captorhinomorphs Gephyrostegid anthracosaurs Scincosaurid nectrideans Tuditanid microsaurs "Dendrerpetontid" temnospondyls Dissorophid temnospondyls	Petrolacosaurid diapsids Edaphosaurid pelycosaurs	
Omnivores	Gymnarthrid microsaurs Pantylid microsaurs		Diadectid cotylosaurs

Note: Size categories are based on estimated total body lengths of largest specimens, small < 0.5 m, intermediate 0.5–1.5 m, large ≥ 1.5 m.

nivores of table 5.3, at least had some abilities to exploit low-fiber plant tissues, such as reproductive organs, megaspores, seeds, and shoot buds, in addition to animal prey. Because the nutritional value of these structures would have been high, it is conceivable that some animals may have survived on them alone.

As a whole the Stephanian records the emergence and diversification of amniotes as the dominant predators and the possible beginnings of tetrapod herbivory among diadectid cotylosaurs. Early amniotes and possibly cotylosaurs appear to have been tolerant of a wide range of environmental conditions. For example, some of the Stephanian amniotes preserved with xeromorphic plants in North America are found also in coal-bearing limnic basins of central Europe. That these same tetrapod groups persisted and were widespread well into the Early Permian suggests that a cosmopolitan terrestrial vertebrate fauna was established before the end of the Carboniferous.

6.4 Synthesis

The Late Carboniferous landscape was complex and spatially heterogeneous, encompassing a variety of ecosystems, each with distinctive attributes. Despite levels of complexity that rival those of later times, the dynamics of Late Carboniferous ecosystems are unlike those of the post-Paleozoic. Most notable is the continuation of detritivory as the major entry point of plant productivity into animal food webs, with expanding, but still limited, herbivory. Plant communities continued to be composed of a mixture of different major groups of vascular plants. The taxonomic structure of the landscape was not randomly distributed across habitats; rather classes were distributionally centered in specific habitats, an ecologically primitive pattern remaining from the much older radiation of plants in the Late Devonian and Early Carboniferous. Post-Carboniferous ecosystems became increasingly dominated by seed plants in all habitats. Tetrapod assemblages also retained patterns established earlier and continued to be dominated by insectivores and carnivores. Clearly terrestrial vertebrates depended heavily on an invertebrate food source, mainly insects, and in this sense there appear to have been much stronger linkages between these animal groups than between the vertebrates and plants.

The Late Carboniferous, particularly the Stephanian, records glimpses of the change that was to occur in the terrestrial biota during the Permian. Traces of floras with xeromorphic elements from peripheral extrabasinal habitats are detectable beginning in the early Westphalian throughout Euramerica. Likewise, there is evidence of distinct vertebrate assemblages within various lowland environments during the Stephanian. Unfortunately the record is confounded by limited exposure of drier tropical habitats and of paratropical areas in general. It is clear, however, that the wetland terrestrial biotas of the Westphalian are minor elements, missing from most areas during the Early Permian.

Vegetational Patterns

Most Late Carboniferous fossil plant assemblages were deposited in or near coastal wetlands (distributory channels, estuaries, interdistributary bays, peat swamps; see chap. 2). These wetlands were physically complex areas that included peat and mineral-soil swamps, floodbasins, and levees; within these areas many microhabitats and associated floras have been detailed (peat-forming habitats: Smith and Butterworth 1967; Peppers 1979; Phillips and DiMichele 1981; DiMichele and DeMaris 1987; DiMichele and Phillips 1988; DiMichele and Nelson 1989; Eble et al. 1989; Feng 1989; Pryor 1988; Raymond 1987, 1988; Raymond and Phillips 1983; Winston 1986, 1988, 1989, 1990; Winston and Stanton 1989; Mahaffy 1985, 1988; Eble 1990; Eble and Grady 1990; Grady and Eble 1990; Bateman in press; Willard in press; clastic-soil habitats: Oshurkova 1974, 1978; Besly and Fielding 1989; Gastaldo 1982, 1986a, 1986b, 1987, 1988; Scott 1977, 1978, 1979, 1984; Wnuk 1986; Wnuk and Pfefferkorn 1987). The vegetational structure and patterns of taxonomic dominance and diversity differed spatially among these habitats (Oshurkova 1974; Scott 1978; DiMichele et al. 1985; Gastaldo 1988), and within any one of them through time (Phillips et al. 1974, 1985; Phillips 1980; Pfefferkorn and Thomson 1982). Enough is known about the ecologies of individual species and the communities they comprised to suggest that long-term persistence of assemblages over millions of years within any one kind of habitat was the rule rather than the exception. Temporal changes between different dominance-diversity patterns appear to have been relatively abrupt rather than continuous and gradual, and were possibly forced by changes in the physical environment rather than by biotic competition (Phillips and Peppers 1984; DiMichele et al. 1987).

Coexisting with wetland habitats as far back as the earliest Carboniferous were peripheral areas that were well drained or, in some cases, seasonally dry. In the Late Carboniferous record, these areas appear to have been part of a continuum of environmental variation, although floristic overlap was limited. Floras from such habitats are relatively uncommon in the fossil record. Included are the large Namurian-age Rock Island floras (Leary and Pfefferkorn 1977; Leary 1981), and tropical-to-paratropical floras from the Namurian through Stephanian of the western United States (Manning Canyon Shale and Moab floras, Utah: Tidwell 1967, 1988; Spotted Ridge flora, Oregon: Mamay and Read 1956; several floras in New Mexico: Ash and Tidwell 1982; Mamay and Mapes in press; Garnett, Hamilton, and Baldwin floras of Kansas: Cridland and Morris 1963; Winston 1983; Rothwell and Mapes 1988) and several areas of Europe (Kerp and Fichter 1985; Broutin et al. 1990). In comparison to contemporaneous wetland floras, these assemblages often contain or are dominated by genera and species that are unknown from peat-forming wetland assemblages. In general they suggest that the plant composition of the more distal wetlands, of better-drained areas, or of areas with seasonal dryness was distinct from that of basinal wetland habitats in the Euramerican tropical belt. Many of these floras were dominated by seed plants and later ones, of Stephanian age, were enriched in conifers, taeniopterids, and other genera that were typically absent from coeval wetland assemblages.

Within the wetlands, Westphalian plant communities had reached a level of structural complexity comparable to that of extant plant communities. This inference is based on the number and kinds of canopy trees, the distribution of ground cover, and the occurrence of epiphytes and vines. Subsequent Carboniferous landscapes were not as structurally complex; for example, Stephanian peat swamps had considerably fewer structural components than those of the Westphalian. In addition there was a strong taxonomic component to the local variability of Westphalian landscapes. At no subsequent time have so many higher taxonomic groups of plants been dominant at the landscape level or partitioned the landscape so strongly along taxonomically specific, ecological lines. This taxonomic-ecologic partitioning began to break down during the Westphalian-Stephanian floral transition.

The signal of change to come began in the late Westphalian with the rise of tree-fern dominance in some compression-impression (floodbasin) assemblages (Pfefferkorn and Thomson 1982). It was approximately at this same time that the earliest floras rich in conifers began to appear sporadically within lowland settings (McComas 1988; Lyons and Darrah 1989). Conifers are known earlier only from transported materials, supposedly derived from "distant" areas (Scott and Chaloner 1983). In peat-forming swamps, which appear to have been more buffered against extrinsic changes than most mineral-soil habitats (DiMichele et al. 1987; Knoll 1985), major floristic changes also began in the latest Westphalian. Westphalian peat swamps were taxonomically distinct from the surrounding lowland vegetation of mineral soils (DiMichele et al. 1985), but during the floral transition to the Stephanian, major extinctions occurred in the lycopsids (Phillips et al. 1974) and tree ferns (Lesnikowska 1989) of peat swamps, and probably in pteridosperms as well (Taylor 1965). The combination of a rise in tree-fern abundance and the sporadic appearance of conifers in mineral-soil habitats, along with a dramatic change in peat-swamp vegetation from lycopsid to tree-fern dominance, strongly suggest physical changes in lowland habitats. Throughout the lowlands, the rise of tree ferns brought in the first potentially closed canopy forests. Tree ferns, as major litter producers and as targets of insect herbivory, may have increased substantially the resources available to both detritivorous and herbivorous arthropods.

Tree-fern dominance of the broader wetlands was a short-lived phenomenon geologically, lasting perhaps as much as 6 My. By the late Stephanian, these plants appear to have been increasingly confined to narrow parts of the lowlands as coniferophytes and new kinds of "cycadophytic" seed plants began to appear more frequently in lowland settings (Read and Mamay 1964; Kerp and Fichter 1985; Kerp et al. 1989). By the Early Permian in both Europe and the United States, tree ferns and medullosan pteridosperms remained inhabitants of peat swamps and wetlands but were surrounded by an increasingly different, xeromorphic vegetation (Blazey 1974; Canright and Blazey 1974; Galtier and Phillips 1985; Broutin et al. 1990). This reflects a broad trend that continued into the Permian, a trend in which xeromorphic forms replaced more hygromorphic to mesomorphic elements of the vegetation (Ziegler 1990).

Animal Assemblages and Plant-Animal Interactions

The animal component of Late Carboniferous ecosystems can be divided broadly into four groups: detritivores, omnivores and herbivores, insectivores, and carnivores. Arthropods comprised almost all of the detritivores and probably accounted for most of the herbivory. Predatory arthropods also were abundant. Tetrapods were mostly insectivorous and carnivorous. By inference, the interactions among these animals, expressed in the likely trophic relationships among them, were very highly developed and complex and cannot be viewed as a simple, or even necessarily a primitive, system. In comparison with later systems that include tetrapod herbivores, the fundamentally different insectivore-carnivore tetrapod assemblages represent an alternative form of energy transfer and trophic organization within highly vegetated ecosystems.

Arthropod detritivory remained the major entry point for plant productivity to animal food webs. A variety of litter feeders is known, some very large or with what appears to be armor; either large size or armor would have deterred many predators. Some forms of insect herbivory were probably well established in the Westphalian, particularly sap feeding, predation on pollen-or-spore-producing organs and seeds, and perhaps leaf mining. Evidence for folivory is less clear; damaged foliage is scarce, and it usually cannot be determined if the damage was done during the life of the leaf or after it became part of the litter. Insect mouthparts suitable for eating leaves also are suitable for consuming litter and other insects. The most convincing evidence is the wide variety of features developed by plants that could serve, even if by happenstance, to deter insect predation. To the extent that detritivores depended on decomposers rather than plant detritus itself, the advent of insect herbivory served to simplify food webs. Modern trophic structure, however, did not appear prior to significant foliar herbivory by tetrapods in the Permian.

Throughout the Westphalian and through much, if not all, of the Stephanian, tetrapod faunas lacked herbivores and were composed almost entirely of insectivores and carnivores with some potential omnivores. None of the known Westphalian tetrapods appear to have been capable of foliar herbivory.

Omnivory may have existed: small amphibians with jaws capable of puncture-crushing invertebrates could have dealt with tough, brittle seed coats or cones, and the low "metabolic size" of these animals would have permitted them to survive on such a diet. However, the amount of energy transferred to animal food webs through such means would have been small. In the Stephanian, diadectids may have had some impact as omnivores or herbivores. Diadectid remains are almost universal in Stephanian fossil assemblages of Euramerica, but they are not particularly abundant in any one assemblage, and their diversity is low. Even if they were herbivorous, diadectids probably effected only low rates of transfer of energy and protein into tetrapod food webs.

The interactions between animals and plants, and hence their mutual linkages and reciprocal effects as selective factors, were greater in Late Carboniferous than in Early Carboniferous ecosystems. Although there is evidence of insects using the aerial parts of plants for sites to lay eggs and develop larvae, the major linkage is through insect herbivory, which, with the development of insect flight, brought a whole new range of selective factors to the plants. Most predation appears to have been on reproductive organs, particularly those bearing pollen and spores. The extent of such herbivory, that is, the volume of plant material consumed relative to that available, is impossible to estimate, but the evidence for general foliar herbivory is limited and equivocal. The possible existence of herbivory in drier habitats, where plant tissues could have provided both nutrients and water, requires critical consideration.

Although detritivory may have had some selective effect on plants (e.g., hardened seed coats or chemical defenses of dispersed parts), it points to rather limited interactions between the plant and animal subcomponents of the larger wetland ecosystem. Because nearly all tetrapods relied entirely upon the secondary productivity of arthropods or on other vertebrates for food resources, plants were immediately important only in defining habitat spaces. For plants, except for any disturbance created, vertebrates had limited impact as direct selective vectors, although we cannot rule out even occasional seed predation as shaping plant reproductive biologies.

By the beginning of the Westphalian, many plants evidenced sophisticated mechanical and possible chemical defenses, presumably against pre- and postdispersal arthropod predation. Potential chemical defenses included resins, which occur abundantly in the tissues of medullosan pteridosperms, potentially glandular trichomes of lyginopterid pteridosperms, and mucilages in marattialean tree ferns. Stephanian tree ferns show evidence of damage to live tissue, whereas medullosans do not (Lesnikowska 1989). Mechanical protection may have included hardened seed coats and highly fibrous or sclerenchymatous pollen and spore-bearing organs. Hardened seed coats may have protected against post-dispersal consumption by detritivores. A modern analogue may be the extant *Ginkgo biloba*, which retains many apparently primitive reproductive attributes; pollination occurs prior to dispersal, but fertilization and embryo formation may occur after separation of the ovule from the parent plant, resulting in a very long period between dispersal and germination. Dispersed seeds or ovules would have been a prime target for detritivores, particularly if dispersal occurred in large numbers, as was apparently the case for many Late Carboniferous plants, such as cordaites and many small pteridosperms. Very large seed size, such as that found in the giant pachytesta seeds of some medullosans (Taylor 1965), also may have discouraged ingestion by all animals except large omnivores with crushing dentitions.

It is problematic to attribute the origin of sclerotic nests in vegetative tissues (such as in many pteridosperms or tree ferns), infolded leaves or hairy leaf surfaces, or "armored" stem surfaces (as in some lycopsids) to adaptation resulting from animal predation. These ultimately may have served such a function, but their origins may reflect quite different selective agents or none at all. Many of these basic features appeared in the earliest members of their respective higher taxonomic groups, well before any evidence of insect or vertebrate herbivory.

Ecosystem Complexity and Persistence

The modernization of plant-community dynamics occurred before that of the arthropods or vertebrates. A high level of complexity was reached before the end of the Carboniferous when animal dynamics were far from "modern," which suggests strongly that animals were not necessary for the expression of the basic structural and dynamic aspects of plant communities. Subsequent to the evolution of significant herbivory, animals probably influenced specific plant-plant interactions, although the specific effects of herbivory on modern plant communities are subject to considerable debate.

The wetland ecosystems of the Late Carboniferous, viewed from a shorter "ecological" time scale, do appear to have been persistent for remarkably long periods (2 to 3 My) in terms of taxonomic composition and dominance-diversity characteristics. Overall the persistence of the vegetation is even longer when viewed in ecomorphic terms. This suggests that such communities were resistant to invasion by new taxa with biomechanically superior traits, or that long-term ecosystem persistence suppressed the evolution of biomechanically superior forms by limiting safe sites for their ecological establishment. Biotic change appears to coincide with changes in prevailing climate, which accompanied the formation of Pangaea during the Late Carboniferous and Permian (Stanley 1988; Parrish et al. 1986, Ziegler 1990). Although interpretation of temporal changes within floras and faunas is somewhat confounded (at million-year time scales) by taphonomic factors, a basic signal can be detected: long intervals of persistence punctuated by short intervals of change. These patterns of relative persistence of ecosystems, resistance to biotically induced change, and major response to marked change in extrinsic conditions appear to characterize most of post-Carboniferous time to the present (see chapter 6).

Because of the potentials for plant-animal coevolution, the entire ecosystem must still be seen as impersistent on a time scale of tens of millions of years. Such ecosystems remained susceptible to invasion or disruption by certain major evolutionary innovations, particularly in the animal component. The plant elements throughout the later Paleozoic appear to have responded most to physical disruption of the environment, and taxonomic assemblages persisted for much longer than older assemblages of plants (Knoll 1984). More importantly, plant community dynamics, as far as we can discern them, were more or less modern by the Westphalian. Taxonomic replacements do not seem to have altered the spectrum of dynamics significantly, although they may have changed the specific pattern that was most common. Furthermore, the demise of the wetland floras does not appear to have resulted from invasion and competitive displacement but from wholesale habitat replacement, bringing in a new biota. The evolution of vertebrate herbivory and the diversification of insect herbivores must have selected against certain dynamics, especially patterns of reproduction and energy allocation to reproductive versus vegetative tissue, although there is presently little evidence to suggest that herbivores caused any major, sudden change in the spectrum of possible interactions among the plants. The evolution of vertebrate herbivory in particular appears to have expanded in the drier, more xeromorphic vegetation that moved into lowlands as they dried out.

7 THE PERMIAN

During the Permian, terrestrial biotic patterns characteristic of the Carboniferous gave way to those typical of Mesozoic and younger biotas (Frederiksen 1972). The transition from Carboniferous to Permian floras and faunas was globally diachronous (Knoll 1984) and occurred over an extended interval of time, spanning the late Stephanian and Early Permian. Although the time involved was great, the change was not gradual or geographically uniform within or between basins; the typical Carboniferous and Permian biotas remained largely at the ends of an edaphic continuum during the transition. Increasing spatial heterogeneity and increasing predominance of drier or better-drained conditions in lowland regions brought "Permian-type" assemblages to prominence in the fossil record. The nature of this biotic transition and the complex intrabasinal facies changes have obscured the Carboniferous-Permian boundary in continental rocks (Barlow 1975). Perhaps the best-documented transitional sequences in Euramerica are the Dunkard (Pittsburgh) Basin of the Appalachians (Barlow 1975), those of the southwestern United States (Read and Mamay 1964), southern Spain (Broutin 1981), and the Rotliegendes of central Europe (Boy and Fichter 1982; Kerp and Fichter

1985; Boy et al. 1990). Floristic changes also occurred over an extended period of time in the Angaran region (Meyen 1982) and in Cathaysia (Li and Yao 1982). During this transitional period, there was a reduction in the frequency of occurrence of floras rich in hygrophilous taxa, particularly medullosan pteridosperms, marattialean tree ferns (pecopterids), and sphenopsids; at the same time, floras dominated by conifers, callipterids (some of which had affinities with the peltasperms; Kerp 1982a), and "pteridospermous" seed plants of many new kinds increased. Faunal changes continued in directions first evidenced in the Late Carboniferous, including the ongoing diversification of insects and insectivores, and increasingly specialized feeding adaptations, such as herbivory, among tetrapods.

Accompanying the temporal changes in biotas was an increase in provinciality, particularly detectable in the vegetation (Read and Mamay 1964; Havlena 1970; Chaloner and Meyen 1973; Chaloner and Lacey 1973; Asama 1985; Ziegler 1990). Four major floristic realms have been recognized (Chaloner and Lacey 1973); they represent possibly the greatest amount of global floristic differentiation prior to the late Tertiary. In broad terms these floristic provinces were (1) the Euramerican, which can be subdivided into more typically European and western North American components; (2) the Cathaysian, divisible into northern and southern subprovinces, both closely linked to Euramerican floras; (3) the Angaran (largely Asian USSR), which may have been subdivided into frost-free sub-Angaran and temperate subprovinces (Meyen 1982); and (4) the Gondwanan, in the Southern Hemisphere. Ziegler (1990) has refined this pattern considerably and recognizes ten biomes, the same number and kind found in extant vegetation, varying from tropical rainforest through tundra. Although these biomes can be grouped generally into the larger four floristic provinces, they are better defined floristically than the "provinces" of earlier authors and are related closely to inferred global climatic patterns. Inferred continental positions during the Late Permian are illustrated in figure 5.5.

The vertebrate record, although excellent in some areas, does not provide the same biogeographic resolution as the plant record. To the extent that faunal composition can be determined, terrestrial tetrapod assemblages do not appear to have been subdivided biogeographically, and many genera have remarkably widespread distributions. Differences between European and North American freshwater aquatic records, however, suggest some provinciality.

Increased provinciality and the areal expansion of more mesomorphic to xeromorphic floras have been related to increasing continentality associated with the formation of Pangaea and to waning polar glaciation (Olson 1985b; Ziegler et al. 1981). It has been suggested that the northward movement of many of the major sampling areas of the Northern Hemisphere may have altered regional climates even without the effects of continental agglomeration (Cecil 1990).

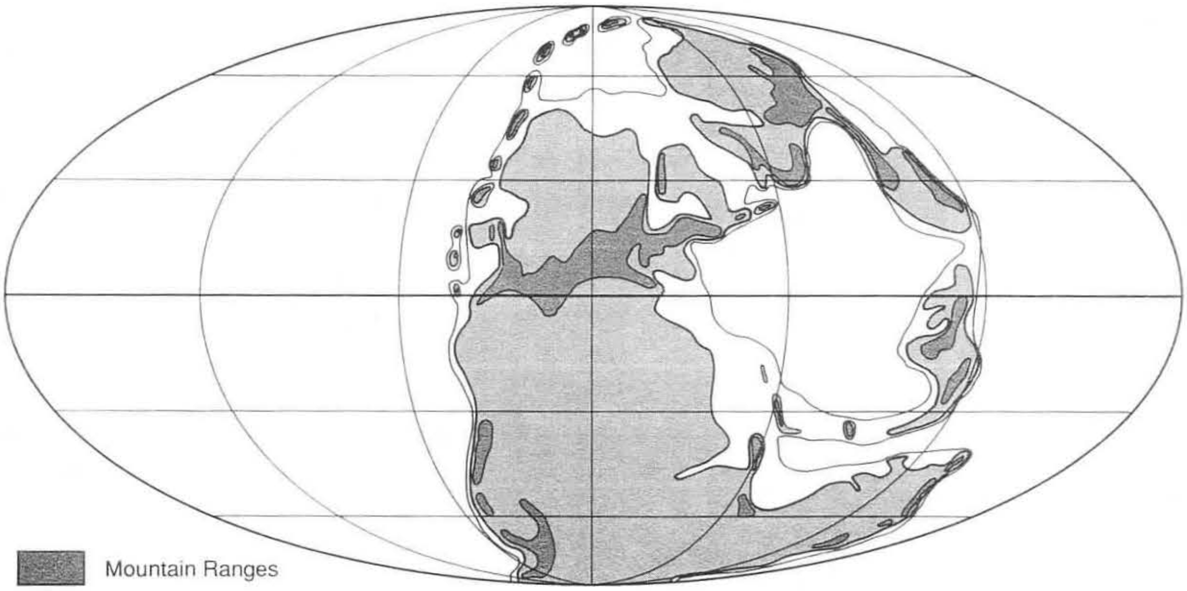
Throughout the Early Permian, only loose links existed between plant productivity and animal food webs, continuing primarily through insect herbivory and arthropod detritivory (Olson 1966, 1967, 1975). Thus, the most conspicuous aspects of ecosystem dynamics also continued from the Late Carboniferous into the Early Permian. The expansion of vertebrate herbivory in the latest Early Permian heralded major changes to come during the Late Permian, when vertebrate herbivory became well established and food webs became essentially modern.

7.1 Plants

Permian vegetation was generally more variable, particularly at the landscape level, than Upper Carboniferous vegetation. At a local level, floristic heterogeneity was very great in some assemblages, with many co-occurring distinctive ecomorphs, representative of different life habits. At a higher level, interregional variability in dominance patterns and ecomorphic diversity became greater during the Early Permian, and appears to reflect greater edaphic variability, and possibly climatic zonation, across the Pangaean continent (Parrish et al. 1986; Ziegler 1990). Tropical and paratropical areas of Euramerica and Cathaysia experienced a great increase in spatial variability of floras, an increase in seed-plant numbers, and a decline in hygromorphic ferns, lepidodendrids, and sphenopsids. Major floristic change occurred earlier in more northern areas, such as the Angaran subcontinent, where a distinct, cordaitean-rich, seed-plant-dominated flora rose to prominence during the Carboniferous, replacing lycopsid-dominated vegetation (Meyen 1982). In some places very wet conditions, associated with peat formation, persisted into the Early Permian and provided sites for the continued dominance of Stephanian-type plant associations (e.g., Appalachian Dunkard Basin); in others, such as southern Cathaysia, Westphalian-type lepidodendrid-dominated peat swamps persisted through the end of the Permian. At the same time, extremely seasonal moisture availability in other areas favored the establishment of a flora strongly dominated by xeromorphic seed plants (e.g., Hermit Shale flora of Arizona).

The earliest Permian floras appear to have retained a strong Late Carboniferous aspect only in areas of high moisture availability. Because many of the European deposits represent disjunct intermontane basins (Havlena 1970, 1975), a relatively high degree of taxonomic variation developed and resulted in floristic changes (compare the floras discussed by Kerp and Fichter [1985] to those discussed by Gillespie et al. [1975]; see Bode [1975] and subsequent discussion). Within peat-forming, basinal areas, floras from the wetter mineral-soil environments were dominated largely by pecopterid ferns, with a large admixture of medullosan pteridosperms such as *Neuropteris* and *Odontopteris*, and few callipterid taxa. Floras dominated by more typically Permian elements, such as numerous callipterids, *Taeniopteris*, and coniferophytes, appeared only sporadically in peat-forming wetlands. The Dunkard Basin, for

LATE PERMIAN (255 Ma)



▩ Mountain Ranges

▨ Lowlands

☐ Continental Shelf

Paleotopography

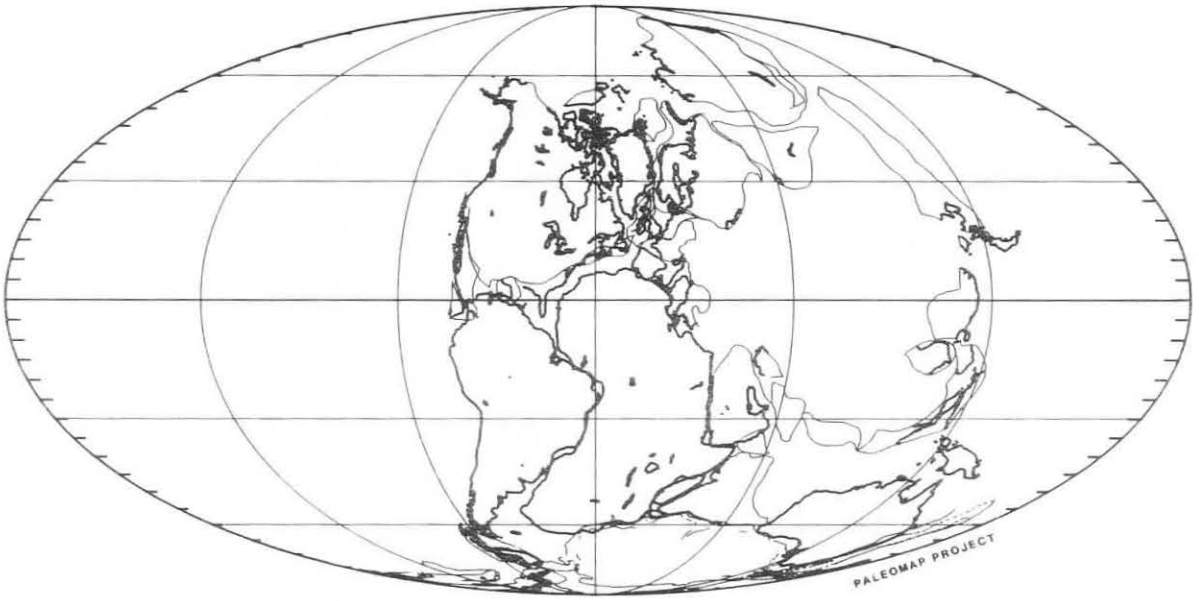


Plate Positions

Fig. 5.5. Generalized continental positions and orography in the Late Permian. (Courtesy of C. R. Scotese and the PaleoMap Project, University of Texas, Arlington.)

example, was sufficiently wet that conifers, most of the callipterids, and many associated plants were rare and were confined to isolated deposits (White 1933; Gillespie et al. 1975).

Early Permian floras from western Euramerica (western United States) were conspicuously enriched in conifers and other mesomorphic-to-xeromorphic plants. During the early Early Permian (Wolfcampian), these western floras retained many taxa typical of the Late Carboniferous, although these became less abundant through time as western Euramerica became increasingly dry.

During the late Early Permian (Leonardian), western Euramerican floras became distinctly different from their antecedents in the region. The development of regional variation was reflected in three distinct floras (Read and Mamay 1964), which contained many plants previously unknown in North America, some possibly linked to Cathaysian floras of China (White 1912; Mamay 1967, 1986; but see Asama 1985). All of these western floras had decidedly more mesomorphic to xeromorphic aspects than older floras of the region. Floristic distinctiveness may derive from regional orogenic activity that altered local climate and created barriers to species exchange within the area (White 1929; Read 1947; Read and Mamay 1964). Judging from current biostratigraphic estimates, no well-known floras of comparable age occur in eastern Euramerica.

The autecologies, life histories, growth forms, and habitats of many Permian plants are poorly known. In the cases of pecopterid ferns, sphenopsids, many medullosans, and lycopsids, analogy to Late Carboniferous antecedents provides a basis for further inference. For other groups, such as conifers, morphology and comparison with better-known younger descendents provide reasonable first approximations of habitat preference and are consistent with broader patterns of distribution. Nonetheless, there has been little attempt to reconstruct Early Permian plant communities (but see Kerp et al. 1989). To the degree that it is now known, the drier parts of the landscape were occupied by conifers and xeromorphic "pteridospermous" plants. Callipterids, taeniopterids, gigantopterids, and some medullosan pteridosperms dominated more mesic, but still seasonally dry areas. Pecopterid ferns, medullosans such as *Neuropteris*, and sphenopsids grew along watercourses or in wetter soils. In the wettest areas pecopterids and the few remaining lycopsids were dominant, with medullosans variably abundant. Thus, there remained a recognizable component of ecological segregation along major taxonomic lines. However, seed plants were clearly a much more conspicuous part of the entire flora than in similar Carboniferous habitats.

Wetlands Patterns

The most conservative Early Permian plant communities were swamps. Palynological analyses of Dunkard Basin coals (Clendening 1974, 1975) indicate a flora rich in ferns, pteridosperms, and sphenopsids, with only small numbers of coniferophytes. Floras of surrounding mineral-soil substrates also retained a slowly changing but strongly Stephanian aspect. Clastic-compression floras in the Dunkard Basin are dominated mainly by pecopterids, medullosan pteridosperms, and sphenopsids, with assemblages of conifers, callipterids, and other more typically Permian plants confined to isolated occurrences (White 1933). Southern China also remained very wet well into the Permian (Ziegler 1990), and included lycopsid, tree-fern, and cordaite-dominated swamps (T. L. Phillips unpublished data), as well as Carboniferous-type assemblages in the adjacent, clastic lowlands (Chaloner and Meyen 1973; Meyen 1982; Laveine et al. 1987). Such wetland floristic conservatism led Clendening to conclude that Dunkard rocks are entirely Upper Carboniferous.

Callipterids and conifers were often conspicuous to dominant in Early Permian intermontane basins of western Europe (Havlena 1975; Kerp 1982b; Kerp and Fichter 1985; Kerp et al. 1989; Broutin et al. 1990), preserved in a wide array of freshwater lowland settings, including lakes and channels, splays, and swamps (Boy and Fichter 1982). In the Dunkard Basin, however, the scattered occurrence of conifers, callipterids, and other "Permian" plants as early as the latest Westphalian or earliest Stephanian (McComas 1988) suggests that a conifer-*Callipteris* flora was established in parts of the lowlands where preservation generally was unlikely but occurred on occasion. The patterns of plant distribution in time and space clearly indicate the contemporaneous existence of a conifer-callipterid flora with a fern-and-pteridosperm-dominated lowland-wetland flora during the Stephanian. It is possible that Permian plants periodically invaded refugial wetlands from surrounding upland habitats, perhaps during brief intervals of increased moisture limitation, establishing ephemeral stands in temporarily suitable habitats (White 1933).

Southwestern United States: Emergence of Xeromorphic Floras

Permian floras of the southwestern United States have been studied intensively and are of considerable interest because they occur with abundant, well-studied vertebrate remains. The oldest plant assemblages of this region are of Wolfcampian age and are rich in pecopterid ferns, medullosan pteridosperms, and sphenopsids. Conifers, *Taeniopteris*, and callipterids also are present, with conifers dominant at some sites (Read and Mamay 1964; Ash and Tidwell 1982; Sander 1987). The morphological-ecomorphotypic heterogeneity among these assemblages suggests considerable variation in the regional physical habitats. At some exceptional sites, such as the Geraldine bone bed in north-central Texas (Sander 1987), there is very high species richness. The Geraldine deposit includes calamites, pecopterid ferns, medullosan pteridosperms, conifers, cordaites, callipterids, questionable lycopsids, and the cycad-like *Russelites* (Mamay 1968) in a mudstone deposited in a single standing-water body. This astounding diversity of ecomorphs seems to represent a mixture of plants drawn from an edaphically diverse sampling area that ranged from very wet to well-drained soils.

Leonardian floras of the southwestern United States have received considerable taxonomic and morphological study and continue to yield new genera and species. Three contemporaneous "floras" existed in the southwest during this time, described by Read and Mamay (1964) as the *Gigantopteris*, *Glenopteris*, and *Supaia* floras.

The *Glenopteris* flora is known only from the Leonardian of central Kansas. The characteristic and dominant plant, *Glenopteris* (Sellards 1908), had very thick, presumably fleshy, leaves. In general, the flora was relatively diverse and included pecopterid ferns, cordaites, lycopsids, and medullosan pteridosperms, among other elements. Mamay (personal communication 1988) suggests a coastal habitat, because the plant-bearing beds are intercalated regionally with marine limestones.

The *Gigantopteris* flora grew to the south, or approximately paleowest, of the *Glenopteris* flora. The *Gigantopteris* flora was highly diverse and included gigantopterids, a group of plants prominent in Cathaysian floras of Permian age, but no *Gigantopteris* itself (Mamay 1986). The flora also included pecopterids, medullosan pteridosperms, sphenopsids, cordaites, callipterids, conifers, and a large number of enigmatic forms, such as early cycads and peltasperms. The dominant plants of the flora vary and include pecopterid ferns, medullosans, conifers, and several different groups of seed plants, broadly characterized as "seed ferns" (Mamay 1967). As with older Permian floras, it is difficult to reconstruct the source communities from existing data. Diverse florules from several localities, such as those described briefly by Ash and Tidwell (1982) or in a series of papers by Mamay (the Emily Irish locality of north-central Texas; Mamay 1968, 1975, 1986, 1988), suggest considerable habitat heterogeneity surrounding the sites of deposition. This is supported further by site-to-site variation in dominance-diversity patterns within florules of the *Gigantopteris* flora. Most plant assemblages from north-central Texas are preserved in drab mudstones that infilled small water bodies within alluvial to coastal-plain settings and probably represent samples of local floras (Read 1943; Mamay 1967, 1968). A number of these deposits are from coastal areas, close to brackish or marine waters (Mamay et al. 1984). If such channel deposits favor the preservation of mesophilous to hygrophilous elements, those species that grew along watercourses will be overrepresented (Scheihing and Pfefferkorn 1984; Gastaldo et al. 1987; Burnham 1989), and the broader landscape may have supported a considerably more xeromorphic flora (see Burnham 1990 for a Tertiary parallel). Most of the plants that appear for the first time in this flora are seed plants, suggesting the increased importance and diversity of this group.

The *Supaia* flora, known from the Leonardian of Arizona, New Mexico and

Utah, was to the approximate paleonorth and paleonorthwest of the *Glenopteris* and *Gigantopteris* floras (White 1929; Mamay and Breed 1970; Ash and Tidwell 1982). It is characterized by a lower diversity: the total number of "whole-plant" species may be as low as 15 to 20. A lack of pre-Permian species is most notable, with no representatives of many of the common earlier Permian groups such as cordaites, sphenopsids, medullosans, and most pecopterids. Most of the *Supaia* flora plants were highly xeromorphic, with leathery leaves, hairy surfaces, spines, scales, sunken veins, and simple, rather than compound, leaves. Seed plants or presumed seed plants overwhelmingly dominate the flora. The best-known florule of the *Supaia* flora is from a channel-fill deposit in the Hermit Shale of the Grand Canyon of Arizona, where plant remains are associated with mud cracks and pseudomorphs of salt crystals, indicative of a seasonally dry climate (White 1929). Some elements of this flora appear in France during the Late Permian.

In summary, the floras of the southwestern United States record great local and regional variation comparable to that of a modern lowland modified by seasonal climatic fluctuations (Ziegler 1990). If this region had received high rainfall throughout the year, as may have been the case earlier, a much more homogeneous flora would have been present because extrinsic conditions would have dampened the effects of micro- and macrohabitat differences (Stebbins 1952; Axelrod 1967, 1972). The Leonardian manifestation of floristic heterogeneity probably is related to climatic conditions that accentuated physical differences within habitats.

Southwestern floras of the United States are the focal point for several inferences about Early Permian biogeography. Most notable are taxonomic overlap between floras of the southwestern United States (western Euramerica) and China (eastern Euramerica), a pattern first recognized by White (1912). Although there are no current paleocontinental reconstructions (e.g., Chaloner and Lacey 1973; Ziegler et al. 1981; Asama 1985) that provide possible migration routes, several Cathaysian taxa, such as *Russelites* (Mamay 1968), and the gigantopterids *Cathaysiopteris*, *Zeilleropteris*, and *Gigantonoclea* (Mamay 1986, 1988), are known from the Permian of the western United States; other plants of this region that may have phylogenetic links to Cathaysian groups include *Delnortea* (Mamay et al. 1986, 1988), *Gigantopteridium* (Mamay 1988), and *Tinsleya* (Mamay 1966). Asama (1985), however, believes that the morphological similarities among the plants from the two regions reflect parallel evolution. Links between the southwestern United States and western Europe are indicated by some plants in the Rotliegend flora of Germany, including *Autunia* (*Sandrewia*) (Kerp 1986) and *Sobernheimia* (Kerp 1983), an early cycad possibly related to the cycads described by Mamay (1973, 1976).

Discussion of the Cathaysian flora and references to literature can be found in Li and Yao (1982). Meyen (1982) provides a synthesis of Angaran Permo-

Carboniferous floras. Archangelsky (1986) discusses Gondwanan floras of Permian age, which are distinct from those of Euramerica, Angara, and Cathaysia.

7.2 Arthropods

The record of Permian arthropods reveals continued diversification of herbivorous insects and evolution or expansion of a number of major groups. Diverse insect assemblages are known from Euramerica (Durden 1984a, 1988), the Kuznetz basin of Siberia, within the temperate portion of Angaraland (Meyen 1982), and from the Late Permian of Australia and South Africa (Wootten 1981). The largest and best known faunas of the Late Permian are from the USSR. Only insects and scorpions have been examined in detail from most of these assemblages (Schneider 1978, 1980, 1982; Wootten 1981; Durden 1984a; Kjellesvig-Waering 1986).

Notable Permian events are the evolution or expansion of hemipterans, sucking forms that fed from phloem or xylem (Evans 1954, 1956; Rasnitsyn 1980), and beetles (Ponomarenko 1969). The beetles (Coleoptera) and bugs (Homoptera) may have evolved in cold temperate regions, as suggested by their distribution in Angaran and Gondwanan deposits, where the floras and sedimentary environments suggest temperature seasonality. As detritivores, herbivores, or pollinators, the beetles opened a spectrum of possibilities for plant-animal coevolution. Also appearing in the Permian were small Diaphanopterodea, which resembled mosquitos in body size, suctorial mouthparts, and structure (Kukalova-Peck 1974), and which may have been bloodsucking forms (Pruvost 1919).

Herbivorous protorthopterans (Carpenter 1971; Burnham 1983) and orthopterans (Sharov 1968) with modern patterns of structural organization, increase in abundance in Permian deposits, as do predaceous ephemeropterans (mayflies) (Kukalova-Peck 1985). Odonates also continue to be numerically abundant as predators (Wootten 1981). Collembolans are documented from South Africa (Riek 1976).

The low number of well-known Permian arthropod assemblages offers an incomplete picture of the ecological roles played by these animals in the Permian. In combination with the Carboniferous record, however, there is enough evidence to indicate that herbivory was global, and that many new groups of herbivores were evolving and dispersing widely, including beetles. The record does not, however, reveal large detritivores like those of the Carboniferous. Many earlier groups, such as millipeds, existed through the Permian, which suggests that detritivores remained important in some, probably most, Permian habitats. Most arthropod-bearing deposits of the Permian are not paleoenvironmentally similar to the peat-forming wetlands of the Late Carboniferous and thus, do not support direct comparison. Permian assemblages generally derive from drier and possibly seasonally cooler settings. A tropical, everwet setting of Permian age may have been dominated by detritivores in much the same manner as Carboniferous wetlands, or modern, equatorial, peat-forming swamps.

7.3 Vertebrates

Early Permian

Our understanding of Early Permian terrestrial vertebrates is derived largely from numerous sites in north-central Texas and adjacent parts of Oklahoma and from several deposits within the nearby Four Corners region of north-central New Mexico, southwestern Colorado, and southeastern Utah. Smaller assemblages are known from northern Oklahoma, Kansas, the Dunkard Basin of the Appalachians, Prince Edward Island (Canada), the English Midlands, and continental Europe. These reptile-dominated faunas appear to have been geographically widespread, with little taxonomic variation among the major land-dwelling forms. Contemporaneous aquatic assemblages from small and large lakes are known, both in North America and continental Europe (Olson 1977; Boy 1977, 1987); the composition of these freshwater faunas varies significantly between the classic Rotliegend and Texas-Oklahoma collections. Although a relatively small sample of terrestrial tetrapods is known from Europe, associated trackway-bearing beds in Germany record a diverse terrestrial fauna (Haubold and Katzung 1978; Boy and Fichter 1982; Fichter 1983; Fichter and Kowalczyk 1983).

The most productive of the more commonly occurring Lower Permian vertebrate deposits in North America represent mudstone infillings of abandoned channels, sometimes carbonate-rich and often termed ponds by various workers (Read 1943; Olson 1958; Berman 1978; Olson and Mead 1982; Eberth 1985, 1987). Characterized by sedimentological evidence indicative of reducing conditions and by channel-like geometries, these deposits yield exceptional specimens of aquatic-to-terrestrial animals and in some cases well-preserved plants and invertebrates. Associated or discrete channel-lag conglomerates often contain a great assortment of generally fragmentary vertebrate remains (Read 1943; Olson 1958; Hlavin 1972; Murry and Johnson 1987). Complete articulated skeletons of terrestrial tetrapods are exceedingly rare and occur most commonly in isolation or in monospecific or very low diversity assemblages within floodplain sediments (Williston 1911; White 1939; Romer 1969; Berman et al. 1987b, 1988). Disarticulated remains of small and almost exclusively terrestrial vertebrates of Early Permian age have been collected in large quantities from fissure fills in southern Oklahoma (Peabody 1961; Olson 1967, 1991; Bolt 1980). Table 5.4 summarizes size categories and dietary groups of Early Permian tetrapods.

MICROSAURS The record of terrestrial microsaurs is sparse, and they have a suite of features that suggests secondarily acquired aquatic adaptations. *Pan-*

Table 5.4 Lower Permian Terrestrial Amphibians and Reptiles

	Small	Intermediate	Large
Carnivores	Eothyridid pelycosaurs Dissorophid temnospondyls Phlegethontid aïstopods	Sphenacodontid pelycosaurs Varanopseid pelycosaurs Seymouriid cotylosaurs Tseajaiid cotylosaurs Parioxiid eryopoid temnospondyls Dissorophoid temnospondyls Ostodolepid microsaurs	Sphenacodontid pelycosaurs Limnoscelid cotylosaurs?
Insectivores	Single–tooth row captorhinid captorhinomorphs Protorothyridid captorhinomorphs Dissorophid temnospondyls Hapsidopareiontid microsaurs Goniorhynchid microsaurs Brachystelechid microsaurs Ostodolepid microsaurs	Single–tooth row captorhinid captorhinomorphs Araeosceloid diapsids	
Omnivores	Bolosaurid reptiles Gymnarthrid microsaurs Pantylid microsaurs	Primitive multiple–tooth row captorhinid captorhinomorphs	Edaphosaurid pelycosaurs? Diadectid cotylosaurs?
Herbivores		Caseid pelycosaurs Advanced multiple–tooth row captorhinid captorhinomorphs	Caseid pelycosaurs Advanced multiple–tooth row captorhinid captorhinomorphs Edaphosaurid pelycosaurs? Diadectid cotylosaurs?

Note: Size categories are based on estimated total body lengths of largest specimens, small < 0.5 m, intermediate 0.5–1.5 m; large ≥ 1.5 m.

tylus, which is well represented in Wolfcampian and Leonardian deposits of Texas, is an exception. This genus had a disproportionately large, massive skull and a dentition that consisted of relatively few, stout, blunt marginal teeth and complexes of palatal and coronoid teeth that resembled the marginal series both in size range and shape. All teeth show wear facets, with some palatal tooth crowns reduced to mere stubs. An unequivocal lack of direct occlusion indicates that the attrition arose from grinding resistant food materials, if not also an admixture of silt and sand grains (Carroll 1968). Whereas the slightly overhanging snout with posteroventrally directed premaxillary teeth suggests a grubbing habit, the entire dentition and powerfully built jaws indicate that food was crushed. The postcranial skeleton includes an expanded rib cage and stout but short limbs that would have held the body close to the ground. *Pantylus* probably obtained food from the soil, and this food may well have included plant roots and rhizomes (Romer 1969), among other resistant plant parts, such as stems and tough-coated seeds. A monospecific suite of more primitive pantylid microsaurs from New Mexico may represent a failed aestivation assemblage (Berman et al. 1988).

The majority of other Permian terrestrial microsaurs are from the Leonardian of Texas and Oklahoma. The marginal dentition of gymnarthrids superficially resembled that of *Pantylus* in consisting of few large, conical teeth, but accessory series were not elaborated greatly, and wear was less extensive (Carroll and Gaskill 1978; Bolt and DeMar 1983). In general, gymnarthrid teeth also were more acuminate, indicative of a piercing, rather than a crushing bite, suited for dealing swiftly with small prey (Gregory et al. 1956). An elongated presacral vertebral column, only moderately developed limbs, and preservation in aquatic as well as terrestrial assemblages suggest that gymnarthrids were less terrestrial than *Pantylus* (Olson 1939; Gregory et al. 1956).

The ostodolepidids were the largest known microsaurs, attaining lengths of greater than 50 cm. Their skulls were strongly wedge shaped with an expanded occipital surface that presumably accommodated a well-developed dorsal axial musculature (Carroll and Gaskill 1978). These features, along with simple, closely spaced, peglike teeth, suggest that ostodolepidids may have sought burrowing prey.

TEMNOSPONDYLS As in the Carboniferous, the greatest variety of terrestrial amphibians during the Permian is found among the dissorophoid temnospondyls. At least ten valid taxa of dissorophoids are known from Lower Permian deposits in Texas, Oklahoma, and New Mexico; although many taxonomic problems exist within this group, as many as four distinct genera are known to occur within single assemblages. The family Dissorophidae shows trends toward increased skull size and the development of extensive dermal ossifications on top of, and in some cases attached to, presacral neural spines. Inappropriately termed armor, these ossifications probably enhanced terrestrial locomotor abilities by strengthening the axial skeleton (DeMar 1966; Bolt 1974a). As a group, armored dissorophoids were of intermediate size or smaller and probably fed on insects and small tetrapods. *Tersomius*, however, lacked dermal armor and was somewhat smaller than other dissorophoids. The remarkable abundance of juvenile *Tersomius* specimens in assemblages that include a significant aquatic component (Carroll 1964a; Olson 1970; Daly 1973; Bolt 1974a, 1977) suggests a change from an aquatic to a terrestrial habit with growth, a pattern that may pertain to other dissorophoid taxa (Olson 1985a).

Trematopid dissorophoids, which are known first from scant records in the Upper Carboniferous, are represented in the Lower Permian by two genera. These small to intermediate-sized forms are interpreted as agile, land-dwelling predators on the basis of marginal dentitions, which consisted of small-to-large acuminate and moderately recurved teeth, and well-ossified but lightly built postcranial skeletons (Olson 1941; Dilkes and Reisz 1987; Dilkes 1990).

The second major group of terrestrial Permian amphibians, eryopoid temnospondyls, is recognized most commonly as a semiaquatic predator. The flat head, dentition, and postcranial anatomy of *Eryops* suggests that this widespread and very long-lived form was crocodile-like in its habits, practicing lie-and-wait predation in or at the margins of water bodies (Miner 1925; Olson 1936; Sawin 1941; Moulton 1974). Although not regarded as a terrestrial predator, *Eryops* was obviously capable of terrestrial locomotion and was certainly preyed upon by large land-dwelling carnivores (Bakker 1982; Olson 1983). *Parioxys*, an intermediate-sized temnospondyl from Texas that is commonly regarded as an eryopoid (Moustafa 1955; Carroll 1964b), was probably a more terrestrial form. In contrast, the various eryopoids known from the Early Permian of Europe appear to have been aquatic ecomorphs (Werneberg 1989; Milner 1989).

COTYLOSAURS (*SENSU* HEATON 1980) The genus *Seymouria* comprises virtually all materials regarded as seymouriamorph cotylosaurs from the Early Permian. First represented in middle Wolfcampian rocks of New Mexico, Utah, and Texas (Berman et al. 1987b) and particularly well known from Leonardian deposits in Texas, *Seymouria* epitomizes a robust terrestrial reptiliomorph of intermediate size (Romer 1928). A generalized dentition of small, fairly uniform, conelike teeth set in modestly constructed jaws suggests a grab-and-gulp feeding style and a diet of soft-bodied invertebrates and small vertebrates (White 1939). A similar form occurs in the late Early Permian of Europe (Martens 1989).

Another fully terrestrial cotylosaur, *Tseajaia*, is known from the Wolfcampian of Utah and New Mexico. Although the described material is larger and more stocky than contemporary *Seymouria* species, these genera share many postcranial similarities (Moss 1972). The more heavily built skull and greater development of premaxillary and caniniform maxillary teeth in *Tseajaia* suggest modest dietary differences between it and *Seymouria*.

Some of the morphologic attributes of diadectid cotylosaurs have been considered previously in the discussion of Late Carboniferous tetrapods. Compared to Stephanian forms, the teeth of Permian diadectids are more specialized and more extensively worn, and their bodies much larger, in some cases exceeding 3 m in length. Their considerable mass and expanded torso indicate a large gut, which together with a low rate of ingestion dictated by a small head, suggests they had the capacity for prolonged chemical processing of a large food mass. Such capacities imply further that a large proportion of the diadectid diet during the Permian may have consisted of large pieces of fibrous plant tissues. As ectotherms, however, they would not have had to process the amount of food required by mammalian herbivores, and such processing may have been quite inefficient by endothermic standards. The basic morphological suite is comparable to that of large, extant, herbivorous tortoises.

The well-documented record of *Diadectes* in the Texas sequence shows an increase in size through Lower Permian deposits (Romer 1944; Olson 1947). Despite intensive collecting efforts in Texas, no diadectid remains have been found in late Leonardian deposits (Olson and Mead 1982; Murry and Johnson 1987).

Fragmentary remains from the Wolfcampian of West Virginia and Colorado have been described as limnoscelid cotylosaurs (Romer 1952; Lewis and Vaughn 1965). More complete materials from slightly younger Early Permian rocks in Germany await description (Martens 1989). These intermediate-to-large carnivorous forms appear to have been capable of movement on land but, like *Limnoscelis*, may have existed mainly as amphibious predators.

AMNIOTES The differentiation of amniotes chartered upon meager occurrences in the Carboniferous is proven in full by the Early Permian record. At least twenty-five amniote genera are known from the Wolfcampian-Leonardian interval of north-central Texas. More than half of these are pelycosaurs, which collectively encompass a very wide range of ecomorphotypic variation. Though there are fewer captorhinomorphs in the Texas-Oklahoma section, they too offer a broad spectrum of ecologically significant adaptations. This array of amniote diversity is expanded further by several curious taxa that cannot be assigned readily to any major group.

CAPTORHINOMORPHS (*SENSU* HEATON AND REISZ 1986). Early Permian protorothyridids from early Wolfcampian deposits of Texas and West Virginia differ little from earlier members of this family of small, agile insectivores (Carroll and Baird 1972; Clark and Carroll 1973). Protorothyridids are last recorded in North America in fissure fillings near Fort Sill, Oklahoma, estimated to be middle Leonardian in age on the basis of the entire tetrapod assemblage (Bolt 1980; Reisz 1980; Olson 1991). A possible younger occurrence of a protorothyridid-captorhinid intermediate is known from a recent discovery in the Upper Rotliegendes of Germany (Martens 1989).

Relatively abundant remains of captorhinid captorhinomorphs from the Early Permian of Texas and Oklahoma record the diversification of a group characterized by massive skulls that had sharply downturned snout tips. Wolfcampian captorhinids were somewhat larger and more heavily built than contemporaneous protorothyridids (Clark and Carroll 1973). Unlike later captorhinids, which had more elongate, rounded snouts and enlarged cheek areas for powerful jaw adductor musculature, these primitive captorhinid genera had relatively high skulls that are triangular in plan view. The maxillary dentition of early captorhinids resembled that of most protorothyridids in consisting of a single tooth row of simple cones spaced between mandibular teeth. More advanced single-tooth-row captorhinids from lower Leonardian deposits had proportionately larger, more closely spaced maxillary and dentary teeth that exhibit distinct occlusal facets (Heaton 1979). The enlarged anterior premaxillary and dentary teeth also show pronounced wear surfaces indicative of shearing bite.

A greater degree of specialization, doubtless related to enhanced food processing, is found in Leonardian captorhinids that have multiple maxillary and dentary tooth rows. Although these superficially resemble the tooth batteries of the microsaur *Pantylus*, detailed study of *Captorhinus* has shown that teeth were variably chisel shaped and that wear was less severe (Bolt and DeMar 1975; Ricqles and Bolt 1983). Rather than crushing and grinding abrasive materials, *Captorhinus* appears to have used its massive jaws to shear food. This multiple-tooth-row plan is elaborated in late Leonardian and Guadalupian (early Late Permian) captorhinids, most of which are large and are regarded as herbivores (Stovall 1950; Olson 1962a, 1962b).

Captorhinids as a group appear to have been fully terrestrial (Heaton and Reisz 1980, Sumida 1989a, 1990), notwithstanding an interpretation of the intermediate-sized, single-tooth-row form *Labidosaurus* as semiaquatic (Olson 1952, 1983). The postcranial skeleton of small captorhinids conforms to a generalized lizard morphotype, and functional analysis of the pectoral limb and girdle indicates a sprawling gait common to primitive tetrapods (Holmes 1977; Heaton and Reisz 1980; Dilkes and Reisz 1986). Whereas the most primitive captorhinids were probably insectivorous, the feeding habits of later Early Permian taxa, particularly genera with multiple-tooth rows, are open to speculation and are described most often as omnivorous. The large, recumbent premaxillary teeth of *Captorhinus* consistently show wear facets on the anterior surface that does not occlude any other teeth (Hotton unpublished data); these large teeth and the hooked, beaklike snout may have been used in some sort of grubbing activity. In foraging, these reptiles may have sought invertebrates among coarse plant litter, or perhaps even in rotten logs, as suggested by the occurrence of galleried wood preserved in captorhinid-bearing sequences. One of the very few records of trophic interaction from the Early Permian is a *Captorhinus* skull that has a partially articulated skeleton of another individual in its mouth (Eaton 1964). "As the two reptiles appear to be conspecific, the specimen constitutes an object lesson on the evils of cannibalism" (Baird and Carroll 1967).

SYNAPSIDS. Nearly all Early Permian terrestrial vertebrate assemblages are dominated by pelycosaurs. From robust forms with small heads and short faces, resembling *Heloderma*, to gracile forms with large heads and long faces, resembling *Varanus*, pelycosaurs ranged from approximately 0.5 m to over 3 m in length, of which half or more consisted of tail. In pose of limbs, configuration of feet, and sprawled gait, Early Permian pelycosaurs were identical to their Late Carboniferous antecedents.

Sphenacodontid pelycosaurs occur in abundance throughout the Early Permian and are known in North America and Europe (Romer and Price 1940; Bakker 1975a, 1980; Olson 1976, 1983). During this time they continued their role as top predators and by the Late Permian attained estimated body weights greater than 150 kg (Romer and Price 1940; Olson 1983). *Dimetrodon*, *Sphenacodon*, and *Ctenospondylus* are characterized by large, laterally compressed, serrate, and recurved teeth set along a well-differentiated marginal tooth row, an enormous gape, and powerful jaws, and were presumably adapted to attacking prey of approximately their own size (Vaughn 1964, 1970; Barghusen 1973; Berman 1978; Eberth 1985). In limb proportions and pedal configurations, these forms were comparable to the largest of the modern lizards (Romer 1922, 1927), and there were no structural features to suggest aquatic habits. *Secodontosaurus*, another Texas sphenacodontid, coexisted with and resembles *Dimetrodon* and *Ctenospondylus* in the development of greatly heightened neural spines that form a "sail" (Romer and Price 1940). Such sails, which also occur in the contemporaneous pelycosaurs *Edaphosaurus* and *Lupeosaurus* (Sumida 1989b), may have served as thermoregulatory organs (Romer 1948; Bramwell and Fellgett 1973).

Varanopseids are the only other reasonably well known group of Early Permian pelycosaurs that can be interpreted confidently as terrestrial predators. Found in the Wolfcampian of New Mexico and the Leonardian of Texas, varanopseids were more gracile than sphenacodontids, reached lengths of approximately 1 m, and conformed to a general lizard morphotype. Teeth were not differentiated to the degree seen in sphenacodontids but were laterally compressed and dramatically recurved in a manner that suggests a very wide gape (Langston and Reisz 1981; Berman and Reisz 1982). Although varanopseid remains are exceedingly rare, taphonomic bias is shown by *Varanops*, which is known solely from a "herd" of some twenty juveniles collected from a single Leonardian-age deposit (Williston 1911; Romer and Price 1940). Taphonomic biases also may be shown by the near nonoccurrence of eothyridid pelycosaurs, a poorly represented but distinct group of small carnivores.

The best known ophiacodontid pelycosaur, *Ophiacodon*, has been regarded traditionally as an aquatic piscivore on the basis of comparatively poor ossification, reduced forelimbs, an absence of claws otherwise characteristic of pelycosaurs, and general skull construction (Romer and Price 1940; Brinkman 1988). Primitive ophiacodontids, such as *Stereophallodon* from the early Wolfcampian of Texas (Brinkman and Eberth 1986), are inadequately represented at present and may include terrestrial forms.

The Early Permian pelycosaur *Edaphosaurus*, like its cotylosaur contemporary *Diadectes*, has the characteristic barrel-shaped trunk and small head of a terrestrial herbivore capable of consuming high-fiber plant tissue. This interpretation of *Edaphosaurus* is weakened, however, by the dentition, which consisted of numerous teeth packed closely along the margins of the jaws and on special palatal expansions that opposed similar batteries on an elaborated medial surface of the mandible. The marginal teeth were slightly larger than the medial teeth, and all were small and bluntly pointed (Romer and Price 1940). Unlike *Diadectes* and advanced captorhinids, wear facets are absent in virtually all specimens. This specialized crushing, not grinding, dentition may have enabled *Edaphosaurus* to feed on small shelly mollusks and arthropods, as well as, or instead of, plant material. If edaphosaurids sought food in shallow, vegetation-choked water bodies or along watercourses, perhaps enough plant material was ingested in the process to supplement a primary diet of animal protein.

The postcranial anatomy of *Edaphosaurus* provides further cause for conjecture. Despite massive limbs unquestionably used for terrestrial locomotion, *Edaphosaurus* is commonly held to be a semiaquatic swamp dweller. This interpretation appears to be predicated largely on the occurrence of well-preserved plants with exceptional and abundant *Edaphosaurus* specimens at a single Texas locality, the remarkable Geraldine bone bed (Sander 1987); in fact most Permian plant-bearing beds of Texas do not represent swamps and do not yield pelycosaurs. Moreover, movement among dense vegetation would have been made difficult, if not impossible, by the full-sized "sail" that was studded with protuberant lateral tubercles. Examples of broken-in-life neural spines are not uncommon, but these in no way define the habit of *Edaphosaurus* or any other "fin-back" pelycosaur. Successive Texas species of *Edaphosaurus*, like several other lineages of large tetrapods in the Early Permian, show progressive size increases during late Wolfcampian and early Leonardian times (Romer and Price 1940).

A close evolutionary relationship between edaphosaurid and caseid pelycosaurs, which was once held to be likely and of no small ecological consequence (Romer and Price 1940; Stovall et al. 1966), has been refuted on the basis of new materials and phylogenetic analysis (Langston 1965; Brinkman and Eberth 1983; Reisz and Berman 1986). Known first from the late Leonardian of Texas, caseids stand alone as the earliest unequivocal "conventional" terrestrial herbivores. The oldest caseid taxon was of intermediate size, but *Cotylorhynchus*, from the Early Permian of Oklahoma, was of gargantuan size, nearly 3 m in length and exceeding an estimated body weight of 300 kg (Stovall et al. 1966). Much of the increased mass was accounted for by an enormous torso that was held close to the ground (contrary to an often-reproduced restoration of Stovall et al. 1966). The entire postcranial skeleton was massive, with particularly robust forelimbs and strong, clawed feet. The rotund body carried a disproportionately small head distinguished by an abbreviated but pronounced snout that bore enormous external narial openings (Olson 1968). In general, the caseid dentition consisted of relatively few, high-crowned, spatulate marginal teeth that became more conical anteriorly. The more laterally compressed teeth were coarsely serrate, like those of herbivorous iguanid lizards, and would have served to cut or slice vegetation. In comparison with *Edaphosaurus*, the development of palatal and mandibular accessory teeth was slight.

The size of the caseid body cavity suggests that large amounts of high-fiber plant tissues were processed through microbial fermentation. Well-preserved hyoid structures known in some genera indicate a large, mobile tongue, and the enlarged external nares indicate an uncertain sensory specialization possibly related to feeding (Olson 1968). Because the rewards of a labor-intensive, digging search for food probably would not have sustained such large animals, the powerful, claw-bearing forelimbs are more likely to have been used in tearing apart aerial plant organs.

DIAPSIDS AND OTHER REPTILES. Remains of Early Permian diapsid reptiles occur in North America and Europe. With general lizardlike body proportions and posture, the best-known genus, *Araeoscelis*, resembled earlier diapsids (Vaughn 1955). This agile form had a modestly differentiated dentition and probably captured hard-bodied invertebrates such as insects (Reisz et al. 1984).

Several small, problematic reptiles from the Early Permian expand the range of ecomorphotypic diversity. *Bolosaurus*, from the Wolfcampian of Texas and New Mexico, and related genera from the Late Permian of the USSR, possessed extremely specialized marginal dentitions (Watson 1954; Ivakhnenko and Tverdokhlebova 1987). The relatively few teeth were highly differentiated and heavily enameled, and the most anterior were somewhat like those of *Diadectes* in being directed anteriorly and chisel shaped. Posteriorly along both upper and lower jaws, the teeth became larger, more bulbous, and variously modified by ridges that pass obliquely from the crown to the base of the tooth. Wear facets were present on most teeth, and those of the cheek series resulted from a shearing pattern of occlusion that "self-sharpened" opposing teeth. The skull and jaw construction suggests a complex musculature that probably was unique among early tetrapods. The bolosaurid postcranial skeleton is virtually unknown.

The front teeth of bolosaurids appear to have collected food materials, which were then sliced, perhaps quite finely, by the cheek teeth. If a specialized diet of "hard vegetation" is accepted (Ivakhnenko and Tverdokhlebova 1987), bolosaurids represent the only small herbivores known from the Early Permian. In *Bolosaurus*, however, the delicate anterior teeth may have been unsuited for removing attached plant structures, and a diet of small invertebrates is perhaps more plausible (Watson 1954).

A single skull from the middle Leonardian of the north-central Texas has recently been declared the oldest therapsid (Laurin and Reisz 1990). Long known as *Tetraceratops*, this unique and exceedingly odd specimen was so named because of numerous cranial rugosities that may have supported hornlike structures similar to those found on later amniote herbivores. The dentition, however, is that of a specialized carnivore, complete with a diastema anterior to an enlarged caniniform tooth. This most unusual form, like later oddities from the otherwise relictual Leonardian assemblage of Texas and Oklahoma, demonstrates that rare and perhaps progressive faunal elements may go uncollected or unrecognized even within the most intensively sampled regions.

CHARACTERISTICS OF TERRESTRIAL VERTEBRATE FAUNAS IN THE EARLY PERMIAN A summary of Early Permian terrestrial tetrapods indicates a variety of feeding habits and considerable diversity within some ecomorphotypic groups (table 5.4). Intensive collecting of deposits in Texas and Oklahoma has demonstrated that two or more taxa of one particular adaptive strategy often coexisted; in particular, the record shows that the depth of various predator guilds was increased significantly during this time. The most diverse assemblages are known from the most productive beds, which are probably early Leonardian in age (Hook 1989). A subsequent decline in small-to intermediate-sized predators has been interpreted as an ecological response to environmental change (Olson 1952, 1983), but this decline may be linked to variations in conditions suitable for the preservation of smaller animals (Olson 1962a; Murry and Johnson 1987).

On the basis of extensive work in north-central Texas and Oklahoma, Olson (1952, 1961, 1966, 1975, 1983) concluded that Early Permian terrestrial vertebrate communities probably relied heavily upon the productivity of aquatic systems. Rather than diminishing through time, this archaic trophic linkage is said to have increased with the apparent decline of insectivores as prey in the latest Early Permian. The recently enhanced record of Carboniferous tetrapods, however, shows that most terrestrial groups of the Early Permian are known first from Stephanian deposits and that a diverse, fully terrestrial tetrapod community existed in the Early Carboniferous. Concurrently, species diversity within aquatic-to-amphibious systems appears to have declined steadily through the Stephanian and into the Permian. These data are difficult to reconcile with the anomalous abundance of top-level carnivores in the Texas record and their postulated dependence on contemporaneous freshwater faunas.

Within the carnivorous and omnivorous feeding categories, several phylogenetic lineages show increases in body size through the Leonardian. This pattern may be indirect evidence of the evolution of herbivores from predaceous ancestors in edaphosaurids, diadectids, and captorhinids, all three of which are represented earlier by smaller insectivorous-to-omnivorous species. Large captorhinids with multiple-tooth rows continued into the Later Permian and occur together with caseids, but edaphosaurids and diadectids apparently were extinct by the end of the Early Permian. Although an immediate phylogenetic antecedent of caseids is unknown, they appear to be most closely related to eothyridids, a poorly known group of small, predaceous pelycosaurs. Thus, adaptations for or at least approaching herbivory evolved independently in several distinct tetrapod groups.

In the later Early Permian, when large herbivorous caseids first appeared, they were not associated with large carnivores (Stovall et al. 1966; Olson 1970); in younger caseid-bearing Guadalupian deposits of Texas and Oklahoma, carnivores are exceedingly rare (Olson 1962a, 1965). Because these caseids and contemporaneous captorhinids are regarded almost universally as herbivores, the late Leonardian assemblages in which they occur may be seen as the earliest record of an herbivore-dominated terrestrial fauna.

Late Permian

Late Permian tetrapod faunas were dramatically different from those of the Early Permian and hence from the rest of the Paleozoic. Herbivorous tetrapods were abundant and diverse, and faunal similarities between northern and southern parts of Pangaea can be recognized (Sues and Boy 1988). Most assemblages were composed largely of mammal-like reptiles. Both terrestrial and aquatic amphibians declined sharply in numbers and diversity. Comparisons between aquatic faunas (Boy 1977, 1987) suggest substantial taxonomic changes and an almost total change between the Early and Late Permian. The abrupt and widely encompassing changes between the Early and Late Permian tetrapod assemblages, terrestrial and aquatic, suggest a global hiatus in the terrestrial fossil record (Boy 1987). In eastern Europe several groups of terrestrial amphibians (eryopoids, dissorophoids) are accompanied by very few aquatic amphibians (e.g., gavial-like archegosaurids). In addition some more or less aquatic families appeared for the first time (melosaurids, ianthanosaurids, dvinosaurids). The first stereospondylous amphibians (alligator-like amphibious-to-aquatic forms) appear in Gondwana (South Africa, India, Australia) and in European and Asian parts of the USSR.

Late Permian tetrapod assemblages are characterized by a high diversity of fully terrestrial diapsids and synapsids (Romer 1973) and a significant reduction in terrestrial amphibians. Included are unquestionable herbivores in large numbers, as well as omnivorous, insectivorous, and carnivorous forms, all abundant and diverse. Tetrapod herbivores occur phylogenetically mainly among the advanced mammal-like reptiles (therapsids), and probably among procolophonids and pareiasaurids. In some South African assemblages, dicynodont therapsids outnumber predatory taxa 10 to 1 (Bakker 1975b), a marked contrast with Early Permian assemblages. Dicynodont head-body size ratios suggest high ingestion rates and an ability to comminute food finely, implying high rates of digestion. Dicynodonts also show evidence of complex behavior, including burrowing (Smith 1987), and of an increased scope of activities. The radiation in herbivores is accompanied by increasing diversity in predators and in reptile ecological diversity. Terrestrial predators such as the gorgonopsids were very vagile, slender forms with high levels of activity (Hotton 1980; Kemp 1982; Sues 1986). The first gliding reptile, *Coelurosauravus*, is recorded from near-shore marine deposits of Europe and Madagascar (Evans and Haubold 1987). These changes indicate the establishment of complex interactions among tetrapods, and between tetrapods and plants. As tetrapods joined insects as herbivores with sizable impact on plant communities, ecosystems reached the spectrum of dynamic interactions that have characterized them since that time.

The dicynodont therapsids formed the first major radiation of herbivorous tetrapods and were by far the most abundant terrestrial vertebrates during the Late Permian (King 1981, 1988; Hotton 1986). They first appeared in lower Upper Permian rocks of South Africa. Dicynodonts left an especially rich fossil record in the Karoo Supergroup of southern and eastern Africa but also have been found in the Upper Permian of Brazil, China, India, Scotland, and Russia (King 1988). They survived the end-Permian extinction, but their early Mesozoic diversity was greatly reduced, and they became extinct in the latter half of the Triassic. The Permian genera range in basal skull length from 50 mm (*Emydops*) to greater than 50 cm (*Rhachiocephalus*) (King 1988). Dicynodonts were quadrupedal animals with short, robust limbs and probably foraged within one meter of the ground, and all shared a stereotyped complex masticatory apparatus that presumably enabled them to be effective herbivores. The skull was rigidly constructed, and the mandibular symphysis is fused. Except for upper canines, the snout was typically edentuous. The rostral ends of both the upper and lower jaws were covered with a horny beak with sharp margins between which food was sliced when the mandible was retracted. Mandibular retraction was facilitated by the laterally widely exposed external adductor mandibulae muscle, and a highly modified jaw joint permitted extensive anteroposterior translation of the mandible relative to the cranium (Crompton and Hotton 1967; King 1981). An elongate trunk, which was posteriorly wide in some forms, and broad pelvic region presumably reflect development of a capacious gut.

Recent work has provided evidence for a considerable range of foraging modes among dicynodonts (Hotton 1986; Smith 1987). *Cistecephalus* and *Kawingasaurus* had distinctive, boxlike skulls and highly modified limbs with structural specializations that are very similar to those in fossorial mammals such as chrysochlorids (golden moles). These small dicynodonts were probably mole-like burrowers (Cluver 1978). Hotton (1986) interprets *Diictodon* as a terrestrial grubber with access to subterranean parts of plants because of its long, clawlike ungual phalanges and the shape of the rostral end of the snout, which he relates to shearing roots and rhizomes; this genus has been found curled up within helical burrows (Smith 1987). Larger dicynodonts, such as *Oudenodon*, may have been browsers that fed on shrublike vegetation, including equisetaleans, pteridosperms with *Glossopteris*-type foliage, ferns, and perhaps low-statured conifers (Hotton 1986).

The Dinocephalia are a group of primitive therapsids of early Late Permian age that includes both herbivorous and carnivorous forms. They were up to 3 or 4 m long, massively built animals, often with considerably thickened bones; they are characterized especially by their peculiar, interlocking incisor teeth (Chudinov 1983; King 1988). Dinocephalians are known from the Dinocephalian Assemblage Zone of the Beaufort Group in South Africa and from the Upper Permian Zones I and II of European Russia (Chudinov 1983). On the basis of body form and taphonomic data, it is inferred that the Tapinocephalidae had a hippopotamus-like, semiaquatic mode of life (Boonstra 1955). They are generally considered to have been herbivores. The dentition consists of numerous chisel-like teeth without clearly differentiated canines. The Anteosauridae, Titanosuchidae, and Brithopodidae were more gracile in build, and judging from the marginal dentition with long canines and robust, conical postcanine teeth, they were predatory forms (Kemp 1982).

Late Permian herbivores also included the Pareiasauria and Procolophonia, both primitive amniote groups of uncertain affinities. Pareiasaurs were large (up to 3 m long), ponderous forms with sprawling limbs; they are known mostly from the Upper Permian of South Africa and Russia. The marginal dentition is composed of relatively simple, laterally compressed, leaf-shaped teeth (Ivakhnenko 1987). The massive trunk region indicates the development of a voluminous gut. Procolophonians were relatively small animals with solidly built skulls and vaguely lizardlike appearance, with short but robust limbs. The orbital margin is embayed posteriorly to accommodate the anterior portion of the extensive jaw adductor musculature. In adult specimens, the more posterior marginal teeth became distinctly expanded transversely. Tooth wear was extensive, producing extensive occlusal surfaces on each tooth in larger species (Ivakhnenko 1979; Carroll and Lindsay 1985). Gow (1978) has argued that only the larger forms had an exclusively herbivorous mode of life and considered the smaller species and perhaps younger individuals of the larger forms mostly insectivorous.

The Gorgonopsida were the top predators in terrestrial environments during the Late Permian (Russell-Sigogneau 1989). The rigidly built, large skulls of these primitive therapsids bore enormous bladelike canines with serrated edges and robust, interlocking incisor teeth (Kemp 1969). The postcanine dentition was greatly reduced. The temporal area for the origin of the jaw adductor musculature was considerably expanded. The limbs are relatively slender and carried the trunk well above the ground (Kemp 1982). A dicynodont jaw has been found between the ribs of at least one gorgonopsian skeleton (Huene 1950).

Another group of carnivorous therapsids is represented by the Therocephalia, which include both robust, short-limbed forms such as the large *Pristerognathus* and smaller, possibly insectivorous forms such as *Ictidosuchoides* (Kemp 1982).

7.4 Synthesis

The Permian terrestrial fossil record differs from that of the Carboniferous in ways that complicate direct comparisons. Two major kinds of biotas overlap in tropical latitudes: that of poorly drained wetlands, characterized by high levels of moisture availability throughout the year, and that of better-drained, probably seasonally dry habitats. These biotas were part of a continuum; the end members manifest dramatic floristic differences, but there are few distinctions among the tetrapod faunas. The Early Permian fossil record documents increasing prominence of the drier-site plant assemblages in lowland depositional environments, a probable indication of shrinking habitat areas for biotas restricted to wetter conditions. As a consequence of this rise in habitat and biotic variability and a proportional increase of difficulty in reconstructing patterns across the landscape, we rely heavily upon sequences that were either poorly drained or that were at least seasonally dry in order to isolate the end members. A combination of complex ecosystem patterns, paleobiogeographic variation, and in some cases inadequate data complicates ecological inferences.

Havlena (1970) subdivides Permo-Carboniferous tropical floras into a hierarchy of progressively more restricted ecological units. The most geographically encompassing units are the "close-to-the-sea" and "intermontane" biomes or ecotopes. The close-to-the-sea biome is far better known and accounts for nearly all of the plant fossil record. Within each of these biomes are floras from predominantly aggradational ("basinal") environments, including swamps, and from predominantly erosional, better-drained ("extrabasinal") environments; the former are much better preserved and hence provide most of the lowland plant fossil record. The character of these aggradational lowlands changed as seasonal dryness in the lowlands became more widespread; in effect, the lowlands of the Carboniferous were also "wetlands," whereas the Permian lowlands became more seasonally dry in many areas.

The general pattern that began in the Stephanian and continued into the Permian is the movement of floras from predominantly erosional or better-drained portions of the landscape into the more mesic-to-hydric aggradational portions of lowland areas. Whether this pattern of species migration can be extended to the larger biomes, with movement from intermontane areas into the close-to- the-sea habitats, is not certain but is suspected for groups such as conifers, which have a scant but definitive record prior to the Stephanian, out of range of all but the most exceptional preservation (Scott and Chaloner 1983).

Throughout most of the Permo-Carboniferous, the vertebrate record does not offer clear evidence for such a mechanism of faunal change. The unexpected appearance of several amniote groups in the late Leonardian and early Guadalupian, however, has been attributed to a pattern of community evolution similar to that described for the plants (Olson 1962a).

Plant-Animal Interactions

The complexity, regional variation, and temporal fluctuation in environmental conditions within Early Permian lowlands suggests a mosaic of ecosystem patterns. Included was the persistence of Carboniferous-type plant-animal interactions and animal food-chain organization in the most stable wetland areas, particularly those of the earliest Permian. In general, however, there were major changes in ecosystem dynamics that began in the Early Permian, most notably the rise of tetrapod herbivory, that led to nearly complete modernization of basic terrestrial ecosystem dynamics by the Late Permian.

Sometime during the late Wolfcampian (middle Early Permian), seed plants became dominant in all areas but those with moderately wet soils. The high diversity of seed plants, particularly a great array of "cycadophytic" forms along with the conifers, suggests further floristic subdivision of better-drained lowland areas than was common in earlier Permo-Carboniferous times. Most of the plants were xeromorphic, even armored in the seasonally driest areas, and would have presented animals with a formidable problem in processing and digestion. As long-lived trees, woody conifers and many of the cycadophytes were much more K-selected than dominants of earlier floras, their more r-selected ancestors. They had greater investment in relatively expensive woody tissues and thick evergreen foliage than did lower vascular plants such as tree ferns. For early herbivores, with limited capacity to reach elevated plant parts, much of the primary productivity of these trees would have been inaccessible. It is unlikely that tetrapod herbivory was a significant selective force in shaping the morphologies of Early Permian trees.

In contrast, plant-insect interactions appear to have modernized considerably during the Early Permian. Little direct evidence has been presented, but the appearance of major groups such as beetles suggests expanded herbivory. The main impact of insects may have been as small, highly specialized herbivores that had a selective effect on plant micromorphology, and possibly even on population structure. The degree to which arthropod detritivory remained dominant in the Early Permian requires investigation, particularly in drier habitats. Detritivory undoubtedly remained important, although insect herbivores may have begun to displace detritivores as the main entry point of terrestrial-plant productivity into animal food webs.

Adaptations for tetrapod herbivory and omnivory were conspicuous in the Early Permian. The impact of herbivores and omnivores, given their limited reach, must have been mostly on ground-cover ferns, sphenopsids and small pteridosperms, shrubby seed plants, and young plants of all types. Folivory may have evolved independently in at least four tetrapod lineages during this time, and in at least another four between the mid-Permian and the Triassic. This pattern suggests responses, probably in the Leonardian, to new ecological opportunities, possibly the spread of xeromorphic, shrubby vegetation with energy-rich leaves, a general increase in nutrient availability, and perhaps distinct growing seasons.

Plant-animal integration within Early Permian ecosystems was increasing, but still reflected mostly plant-insect interaction, through herbivory and possibly pollination. Arthropods still appear to have been the link between plants and vertebrates within the larger ecosystem. This is reflected in the continued dominance of tetrapod assemblages by carnivores and a variety of insectivores into the middle Leonardian, despite the emergence of vertebrate herbivory. The available evidence for most animal groups indicates increased overlap and specialization within ecological roles first defined in the Late Carboniferous. To the extent that tetrapods depended on insectivory and carnivory rather than herbivory throughout most of the Early Permian, tetrapod food chains retained a primitive character.

Early Permian ecosystem structure and dynamics were clearly intermediate between those of earlier Paleozoic and Mesozoic ecosystems. Floras show increased physiognomic and taxonomic affinities with the Mesozoic, whereas general trophic interactions remain Paleozoic in aspect. The evolution of tetrapod herbivory in the late Early Permian opened the possibility for radical changes in the pattern of energy flow to higher trophic levels. The major effect of vertebrate herbivory was to shorten the length of food chains and thus to increase the amount of energy from plants available to higher-level consumers. As the sophistication of herbivory increased, herbivores undoubtedly became major selective forces that shaped plant phenotypes and community structure. Judging from the extent of vertebrate herbivory in Guadalupian deposits (Late Permian), it appears that ecosystems had undergone significant modernization before the Late Permian, and that plants and animals were linked in a more singular set of interdependent dynamics based on plant primary productivity.

8 PALEOZOIC SUMMARY AND DISCUSSION

The Paleozoic was the time during which terrestrial ecosystems were organized and assembled. The plants, invertebrates, and tetrapods can be thought of as three separate subsystems of the larger terrestrial ecosystem. Dominance-diversity patterns, structure, and interactions within these subsystems modernized more or less independently and at different rates throughout most of the Paleozoic. Concomitantly, these three separate subsystems became integrated through trophic interactions and the creation or modification of habitat conditions. This partitioning of ecosystems into "phylogenetic" subunits differs radically from the organization of highly integrated modern systems.

The appearance of structurally and ecomorphically modern plant communities in some parts of the landscape primarily during the Late Devonian and Early Carboniferous included the evolution of life histories, particularly seed habit, that permitted the exploitation of a wide variety of terrestrial environments. The independent evolution of arborescence in nearly all major groups of plants was key to the development of multistratal forests in some habitats at this time. By the Late Carboniferous, complex forest structure and a wide variety of forest profiles and dynamics were clearly in existence across all major land masses.

Global provincialization of vegetation began during the Early Carboniferous and increased more or less continuously until the Permian, when it reached its Paleozoic maximum; this was perhaps the greatest provincialization known prior to the later Tertiary. Such provincialism was made possible by several factors. The physical opportunities increased in diversity and abundance during the Paleozoic as environments changed globally. Because the plants were at the base of the major terrestrial radiation, they evolved increasing tolerances to demanding physical conditions and expanded the extent of the vegetated land surface. This expansion into unoccupied parts of the terrestrial environment was accompanied by an increase in local and regional vegetational heterogeneity, a consequence of local variation in both physical conditions and evolutionary dynamics.

The first animal groups to exploit plant productivity were the arthropods, and then primarily as detritivores. Detritivory was the main entry point of plant primary productivity into animal food webs until the end of the Early Permian. Herbivory, largely by insects, is known from the Early Carboniferous and may have existed in the Devonian. Herbivory expanded rapidly during the Late Carboniferous and was an established part of ecosystem dynamics by the Stephanian or possibly late Westphalian and into the Early Permian. As suggested by the large size of medullosan pollen, insect pollination probably had evolved by the Westphalian. The selective effects of arthropods on plants may be seen in the evolution of sclerotic seed coats and other structural features that would have served to deter post- and predispersal predation. Clear evidence of damage to living foliage does not appear until the later Westphalian.

Tetrapods were the final element to enter the web of interactions in terrestrial communities. They began, and continued, as carnivores and insectivores through the Carboniferous and Early Permian, situated at the ends of long food chains that were mediated primarily by arthropod detritivory. Although predation on insect herbivores would have shortened some of these pathways and added trophic links to the system, it was not until the expansion of tetrapod herbivory in the late Early Permian that a full integration of the three subsystems was established. The integration had progressed greatly by the Late Permian. However, even by the end of the Paleozoic, the tetrapod component of ecosystems was distinctly different in the sizes, modes of feeding, and range of resources exploited from Mesozoic and younger ecosystems.

8.1 Ecosystem Stability and Persistence

The fossil record affords an opportunity to examine ecological patterns over extended periods of time, periods much greater than those accessible to any neoecological studies. Although there are flaws in this record that limit resolution and the kinds of questions that can be addressed, basic patterns are evident.

The evolution of terrestrial ecosystems during the last half of the Paleozoic encompasses 150 to perhaps as much as 200 My. The modernization of terrestrial communities that occurred during this time was neither rapid nor an unbroken continuum. Evolutionary innovation played a major role in the process, modified by global changes in environmental conditions and by dramatic changes in the interactions among organisms on the land surface. In addition, as ecosystems became increasingly complex, the complexity itself appears to have had a role in constraining the kinds of structural changes that could be further accommodated, and hence the direction of evolutionary events.

The times of greatest change in ecosystem structure were the Late Devonian and the earliest Early Carboniferous, and the transition from the Carboniferous to the Permian. During the first of these, most major architectural and life-history patterns evolved within plants. These patterns were expressed strongly along taxonomic lines and generally reflect what have been described as classes; as a consequence ecological resources appear to have been partitioned mainly along taxonomic lines. This ecotaxonomic partitioning established a framework for subsequent evolutionary events throughout the Carboniferous and into the Permian. There unquestionably were changes in the taxonomic composition of terrestrial communities during the Carboniferous, most notably the rise of a peat-forming, wetlands vegetation, the evolution of insect diversity, and the appearance of amniotes. Despite these major changes in the constituent plant and animal groups, the basic biotic partitioning of the landscape and its resources remained largely the same throughout the interval.

At a detailed level, the Euramerican tropical biota of the Late Carboniferous graphically illustrates that ecosystems are fundamentally persistent entities if extrinsic conditions remain relatively unchanged. Peat-swamp floras underwent four major changes during this time interval, all on a basic theme that reflects changes in dominance-diversity structure more than fundamental taxonomic change in the vegetation. Profound change in the basic biotic composition of the wet lowlands appears to be driven by climatic change. The effect of evolutionary novelties on the structure of communities, at least as a primary driving force of change, appears to have been minimal. However, by all abiotic indicators, changes in physical conditions were much more gradual than were resultant changes in ecosystems, suggesting that the systems may have had organizational properties that engendered persistence and maintenance of biotic interactions and dynamics until thresholds were crossed. At such times biotic change occurred rapidly. The record indicates that most responses were migrational, but they also may have involved extinction and the establishment of novel phenotypes.

The changes in ecosystem dynamics that occurred during the Permian appear, at least superficially, to be more complex than those of the Devonian-Early Carboniferous. Complex ecosystems were already established, global biotic provincialism was developing or had developed in many groups of organisms, and global climates were influenced by the formation of Pangaea. Changes in plant communities during this time reflect a combination of regional extinction, the loss of many of the dominant lower vascular plants of wetlands, and the rise to dominance of seed plants in most kinds of habitats. This was the final breakdown of a strong, high-level taxonomic overprint on ecological partitioning. Despite the complexity of the global pattern, physical factors appear again to have had preeminence over biotic factors as the ultimate driving force of most ecological change.

During the floristic changes that accompanied the Permo-Carboniferous transition and the changes in faunal dominance-diversity patterns that accompanied them, tetrapod herbivory appeared. As a profound change in the means of energy transfer from plants to animal food webs, tetrapod herbivory may be one of the best examples of how an evolutionary innovation can modify some aspects of otherwise stable ecosystems. The rarity of such events, the restriction of their rise and ecological fixation to relatively narrow intervals of time, and more importantly, their nearly simultaneous occurrence in more than one phylogenetic lineage comprise a pattern repeated for critical adaptations in both plants and animals and one that characterizes both major times of ecosystem change in the Paleozoic.

8.2 Conclusions

1. The assembly of terrestrial ecosystems during the Paleozoic to a large extent dictated the direction of subsequent ecological and evolutionary events and the kinds of interactions possible between plants, invertebrates, and vertebrates. As with species-level evolution, historical constraints play an important role in understanding patterns of ecosystem evolution. The Markovian nature of evolutionary processes insures the influence of Paleozoic events on all younger systems.
2. The Recent is a poor analogue for nearly all aspects of Paleozoic ecosystems except for those of the latest Permian. The lack of tetrapod herbivory, the narrow spectrum of plant-insect interactions, the importance of detritivory as the base of the food chain, and the strong partitioning of ecological resource space along widely divergent phylogenetic lines in plants are themes that run throughout most of the Paleozoic. Because of these and other fundamental differences, ecological models based on the present cannot be applied to Paleozoic examples in a uniformitarian manner.
3. The generality of ecological and evolutionary principles can be tested through attempts to apply them to Paleozoic ecosystems. These principles include persistence, the relationship between complexity and stability, the responses of ecosystems to large-scale extrinsic stresses, and the effects of local disturbances on such processes as succession or persistence. The great differences between the Paleozoic and the Recent in taxonomic composition and in the basic biotic interactions within the ecosystems present us with a unique source of data to use in refining ecological concepts and testing their generality.

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